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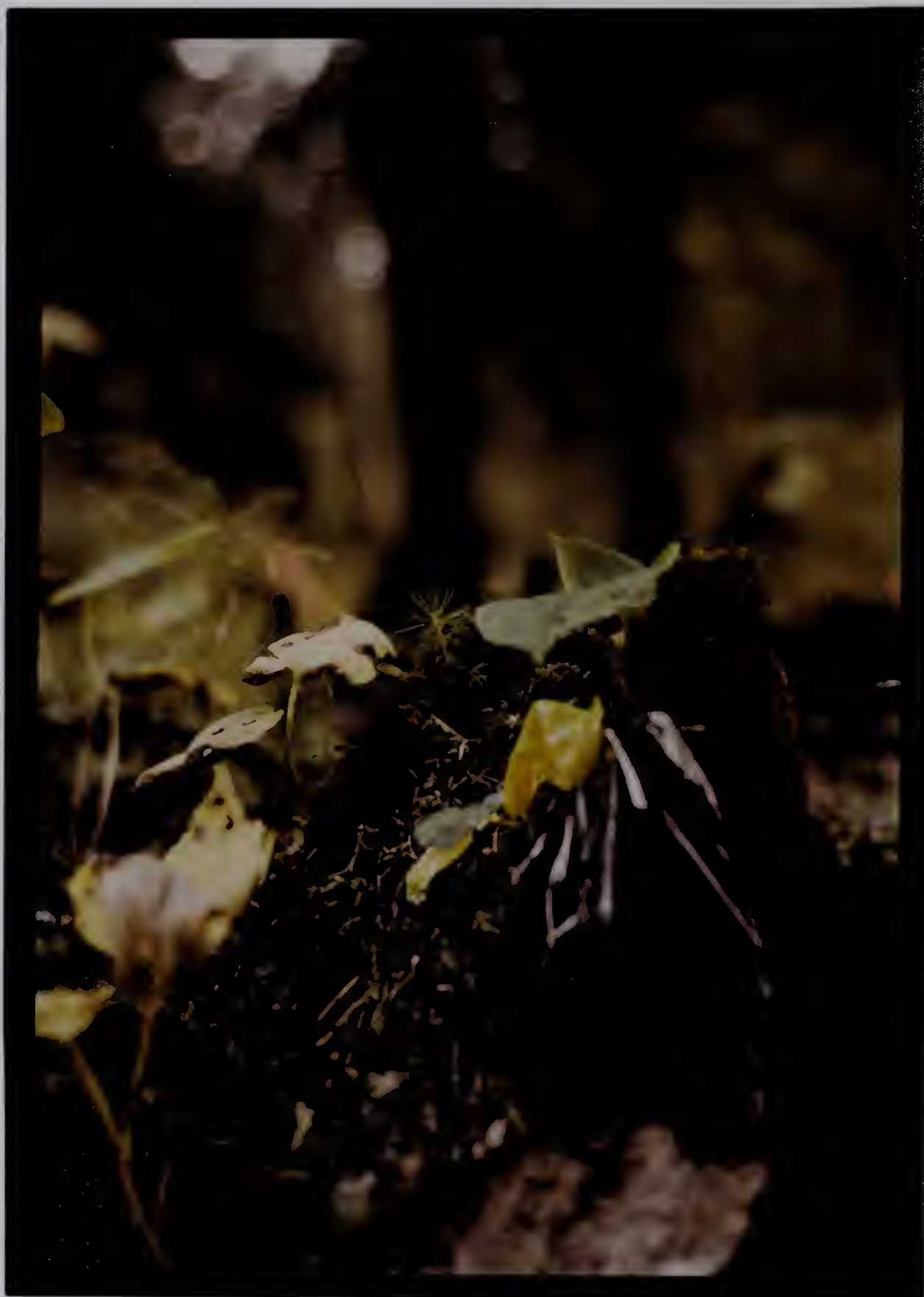
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THE UNIVERSITY OF ALBERTA

ECOPHYSIOLOGY OF WHITE SPRUCE [Picea glauca (Moench) Voss]

REGENERATION



by

EDWARD CARTER TEAR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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IN

FOREST SCIENCE

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ECOPHYSIOLOGY OF WHITE SPRUCE [Picea glauca (Moench) Voss] REGENERATION submitted by EDWARD CARTER TEAR in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in FOREST SCIENCE.

ABSTRACT

The importance of light and seedbed type were evident for germination success and seedling survival of white spruce [Picea glauca (Moench) Voss] in the field. Under forest canopy cover, seedbeds of exposed mineral soil had higher rates of germination than seedbeds with competing vegetation removed or on seedbeds with competing vegetation intact. The shade offered by the forest canopy and the seedbed of mineral soil probably maintain adequate soil moisture conditions to allow good germination. Microsites which had mineral soil exposed and which were only partially shaded enhanced white spruce seedling survival. These microsites probably did not experience severe fluctuations in soil moisture content which may be a major cause of seedling mortality in white spruce.

Time of year, light and watering do not act independently on retention, distribution or partitioning of recently photoassimilated ^{14}C . Seasonal patterns of each are influenced by either light or watering or both. Spruce seedlings grown under water stress or "full-light" conditions retain less ^{14}C than those seedlings grown under no water stress or grown under low light. The effects of light or watering regime are more pronounced on first-year seedlings than on second-year seedlings.

Generally, second-year seedlings translocate a greater percentage of recently assimilated ^{14}C to the roots than do

first-year seedlings. The percent of ^{14}C translocated to the roots varies with time of year and is affected by the interactive effects of light and watering.

Between June and September an increasing proportion of assimilated carbon-14 is channelled into storage rather than into structural components. Deviations from this pattern can occur as a result of changes in light and watering.

Xylem pressure potential can be used to estimate white spruce seedling survival. The relationship between xylem pressure potential and survival varied with soil type, probably due to differences in hygroscopic properties. The younger the seedling the more sensitive it is to drying soils.

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I. INTRODUCTION

Regeneration of a species is one of the most difficult objectives to attain in forest management. Adequate ecological conditions for germination and establishment of the desired species are required if the species is to be able to restock the area. These conditions can be provided by careful choice of the harvest method. However, the choice of the cutting method is influenced by a complex of biological, physical and economic considerations (Smith 1962). In many cases, the harvest cut chosen may not provide suitable ecological conditions for adequate natural regeneration.

The intensity of the harvest cut ideal for stimulating reproduction of a given species is usually based on the tolerance of the species. Generally, tolerance refers to the inherent ability of a species to grow in an understory (Spurr and Barnes 1973). There are several difficulties with such a classification.

1. Tolerance may differ from site to site indicating genetic variation or phenotypic plasticity.
2. Tolerance changes with age.
3. Tolerance to low light does not imply tolerance to moisture stress.
4. Other environmental factors which may be as important as light and moisture are disregarded.

White spruce [Picea glauca (Moench) Voss] is classified as a tolerant species (Spurr and Barnes 1973), and is found on a wide range of sites (Fowells 1965). Natural regeneration of logged white spruce sites is generally considered to be inadequate and slow (Blyth 1955, Candy 1951, Quaite 1956, Sutton 1969). This is true even with an ample seed source (Crossley 1955). According to Jarvis et al. (1966) white spruce will germinate on a wide variety of seedbed types and exposures. Others have found that the rate of survival declines rapidly during the first 2 to 3 years (Ackerman 1957, Crossley 1955). In Alberta, seedlings are considered established if they have survived 3 growing seasons (Alberta Forest Service 1971).

Before a seedling can become established, the seed must germinate, the radicle must penetrate the organic layer and roots must grow into mineral soil. Prior to making contact with the mineral soil, a seedling is very susceptible to environmental stress.

A. Objectives

Many autecological studies have been conducted to determine the factors affecting success of white spruce regeneration. Several factors have been suggested to explain the lack of success of regeneration on logged white spruce sites. These include; high solar radiation, low soil moisture, high soil temperature, competing vegetation and

lack of exposure of mineral soil. Place (1955) stated that the establishment of white spruce is easier to secure under shaded conditions but growth is greater in the open. Day (1961 and 1964) found that summer heating and drying of the soil surface can be a cause of severe seedling mortality on logged-over subalpine fir [Abies lasiocarpa (Hook)] - spruce [Picea engelmannii Parry X P. glauca (Moench) Voss] sites. Forty percent shade significantly reduced mortality on all seedbed types. McClain and Armson (1975) stated that growth increased with increased moisture. Lees (1972) stated that mineral soil or rotten wood seedbeds and freedom from vegetative competition were required for spruce regeneration.

In many of these studies growth was used as an indicator of the influence exerted by the environment on regeneration success. Because growth is the net result of various metabolic activities, which are controlled both by nutritional and hormonal status of the plant (Rangnekar and Forward 1969), correlations using growth are often weak.

Others have conducted studies using defoliation, girdling and combinations of these techniques to gain insight into the sources of carbohydrates for growth of various parts of a tree at different times of the year (Allen 1964, Kozlowski and Winget 1964, Kulman 1965). These methods are also indirect and have provided weak correlations.

The examination of metabolic processes may help to

explain the success or failure of seedlings. A more direct means of investigating the problem is the measurement of photosynthesis. Ribulose diphosphate is the normal substrate to which CO₂ is added, leading to the formation of phosphoglyceric acid (PGA) one of the first stable products of photosynthesis (Salisbury and Ross 1969). Carbon assimilated by the leaves may be used by the plant in various ways. Some of the carbohydrates, mostly in the form of sucrose (Schier 1970), are translocated to growing regions to become structural components. Others are a source of energy (through respiration) needed in the synthetic processes associated with growth. The remainder is accumulated in reserves which may be used for growth at a later time.

According to Sestak et al. (1971) the use of radioactive carbon dioxide (¹⁴CO₂) has made possible great advances in the study of photosynthesis and much of our knowledge of the biochemical pathways of photosynthetic carbon fixation. Through the use of carbon-14 it may be possible to determine more directly the influence of the environment on various physiological processes of white spruce. The information provided may answer some questions pertaining to success or failure of seedlings.

The overall objectives of this study were to compare success of one- and two-year-old seedlings of white spruce in cutover and uncut areas and to describe some ecophysiological characteristics which influence success of

spruce regeneration.

The first objective was to determine success (survival) of white spruce seedlings in the field as influenced by shelter and seedbed preparation. The second objective was to observe the patterns of retention, distribution and partitioning within white spruce seedlings of carbon assimilated during the first and second growing seasons. Changes due to light and watering were noted. Any changes in these patterns might help to explain the effect that drought and shading have on the success of white spruce regeneration. This was accomplished by permitting one- and two-year-old white spruce seedlings to photoassimilate $^{14}\text{CO}_2$ at different months of the year. A third objective was to determine the relationship between seedling survival and drying soils.

Mortality of natural white spruce regeneration is highest in the first two to three years (Ackerman 1957, Crossley 1955). Of the many causes of mortality, drought is often cited as the chief cause (Day 1964, Place 1955, Rowe 1955, Sutton 1969). Therefore, emphasis for this study was placed on the effect of water relations on seedling physiology.

B. Problem Statements

1. Does retention of photoassimilated $^{14}\text{CO}_2$, forty- eight hours after uptake, vary with time of year, watering and light level?
2. Does distribution of photoassimilated $^{14}\text{CO}_2$, forty-eight hours after uptake, vary with time of year, watering and light level?
3. Does partitioning of photoassimilated $^{14}\text{CO}_2$, forty-eight hours after uptake, vary with time of year, watering and light level?
4. Do the rooting media differ in their effect on survival¹ of one-month-old greenhouse seedlings?
5. Does the type of seedbed preparation and the presence or absence of a canopy influence germination success and survival² of first and second year seedlings?

Some definitions with reference to the above problem statements are as follows;

Retention is the percentage, of carbon-14 fed, which was recovered from the seedlings.

$$\text{Retention} = \frac{(^{14}\text{C uptake} - ^{14}\text{C losses}) \times 100}{\text{amount } ^{14}\text{C fed (2.45 uCi)}}$$

Distribution refers to the percentage of carbon-14 recovered which was found in the roots or shoots.

Partitioning refers to the separation of carbon-14 into one of two fractions; the 80% ethanol-soluble fraction or the 80% ethanol-insoluble fraction. The soluble fraction includes all sugars, starches, amino acids and organic acids

while the insoluble fraction includes the structural components such as cellulose, hemicellulose, lignin and pectin.

Rooting media used in this study were (1) peatmoss - a fibrous acid (pH about 4.5) peat and (2) a "greenhouse soil mix" (3:2:2 - loam, peat, sand).

Survival¹ represents the percentage of seedling surviving, as determined by visual means, for 3 weeks after a particular period of drought.

Xylem pressure potential (XPP) is a measure of the tension with which water is held in the water conducting elements in the plant. It reflects both above and below-ground water status.

Survival² is the percentage of seedlings surviving from one field observation to the next.

II. METHODS

The study consisted of both laboratory and field work. The approach used throughout this thesis is of a comparative nature. Each experiment was designed such that segments are comparable with each other and that each experiment can be related to the others. It was intended that the laboratory work would help explain some of the phenomena occurring in the field.

A. Laboratory Study

1. Retention, Distribution and Partitioning of Carbon-14

First- and second- year white spruce seedlings were grown in 175 ml pots (one per pot) in two growth chambers. The chambers were programmed to simulate conditions at the field study area as closely as possible (Table 1). Seeds from a source near the study areas were used (seedlot DS 5-2-70). All seedlings were subjected to the same monthly maximum-minimum temperatures and photoperiods. Light intensity (400-700 nm) was measured with a Lambda Ins. Corp. quantum light sensor. One half of the seedlings received "full light" ($320 \text{ uE m}^{-2}\text{s}^{-1}$), while the other half received "half light" ($160 \text{ uE m}^{-2}\text{s}^{-1}$), thus simulating a clearcut and an uncut site, respectively. In addition, one half of the seedlings in each light group were watered every 3 days to maintain soil moisture near field capacity. The other half

Table 1: Temperature and photoperiod program for laboratory grown seedlings.

MONTH*	DAY TEMP** °C	NIGHT TEMP °C	PHOTOPERIOD h
JANUARY	4.0	4.0	8
FEBRUARY	4.0	4.0	10
MARCH	4.0	4.0	12
APRIL	6.2	4.0	14
MAY	14.8	4.0	16
JUNE	18.1	7.1	17
JULY	22.8	11.6	17
AUGUST	17.2	7.3	15
SEPTEMBER	12.8	4.0	13
OCTOBER	12.0	4.0	10.5
NOVEMBER	4.0	4.0	8.5
DECEMBER	4.0	4.0	7

*temperatures and photoperiod were changed every 3 weeks.

**a minimum of 4.0°C was attainable in growth chambers.

received water only every 12 days. The degree of plant water stress developed varied from month to month as a function of temperature and photoperiod.

Assimilation, allocation and partitioning of carbon were measured using $^{14}\text{CO}_2$ (Figure 1) and a liquid scintillation counter. Neilson (1977) found little isotope discrimination in conifers to C-14. This makes its use for studies such as this very effective. Each treatment of watering within each light group was replicated four times for each month for first-year seedlings and three times for second-year seedlings.

All plants were allowed one week to acclimate to the simulated climatic conditions before measurements were made. One day prior to $^{14}\text{CO}_2$ assimilation, the plant material was removed from the growth chamber and placed in another

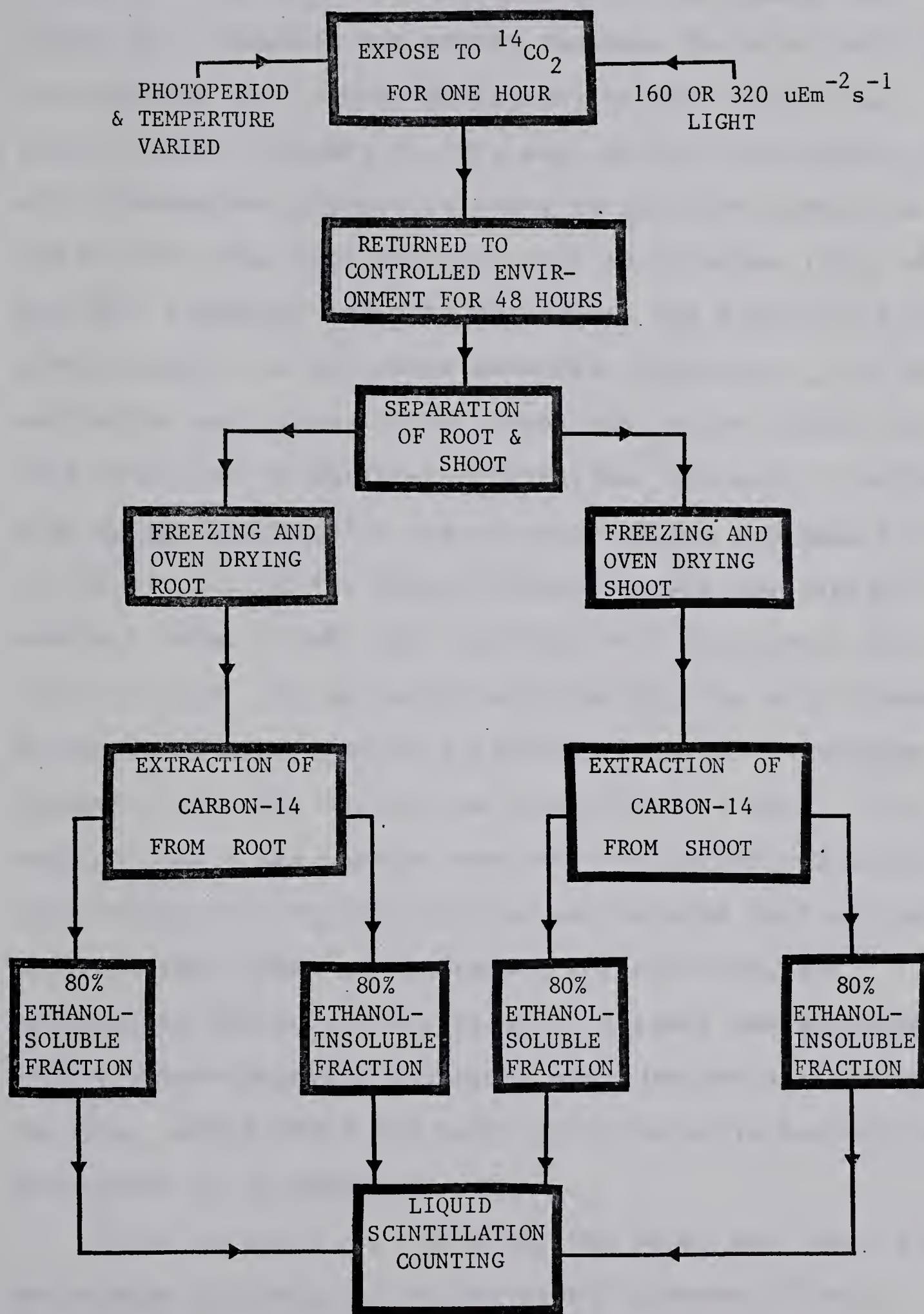


Figure 1. Flow diagram depicting procedures used in determining the short-term fate of carbon-14 in first- and second-year white spruce seedlings.

chamber also programmed to simulate field light and temperature conditions. This second growth chamber was linked to a fumehood for safety reasons. In turn, each plant was isolated in a closed plexiglass chamber within the growth chamber (Figure 2). The soil surface was sealed off with transparent plastic in order to minimize adsorption of CO₂ to the soil. Approximately 2.45 microcuries (uCi) of Na²¹⁴CO₃ (specific activity 59mCi ml⁻¹) was placed in a watch glass adjacent to the plant material. Ursino *et al.* (1968b) and Gordon and Larson (1970) found that young plants are very sensitive to internal irradiation. Exposure of white pine (Pinus strobus L.) and red pine (Pinus resinosa Ait.) to 150-500 uCi of ¹⁴C caused reduced growth and damage to terminal buds. I felt that 2.45 uCi fell far enough below these dosages that no damage would occur. Two millilitres of 85 percent lactic acid were injected onto the watchglass to release ¹⁴CO₂ from the sodium bicarbonate. A small 3V DC fan mounted inside the chamber was used to minimize boundary layer resistance to CO₂ transfer and ensured that all parts of the chamber were at the same ¹⁴CO₂ activity. Air temperature within the assimilation chamber was measured with a telethermometer and thermistor (Yellow Springs Ins. Co. Inc., model 44-TE and model 401). Relative humidity was maintained at 50 percent.

After exposure for one hour, the plant was removed from the system and returned to the growth chamber. It was assumed that one hour was sufficient for the plant to

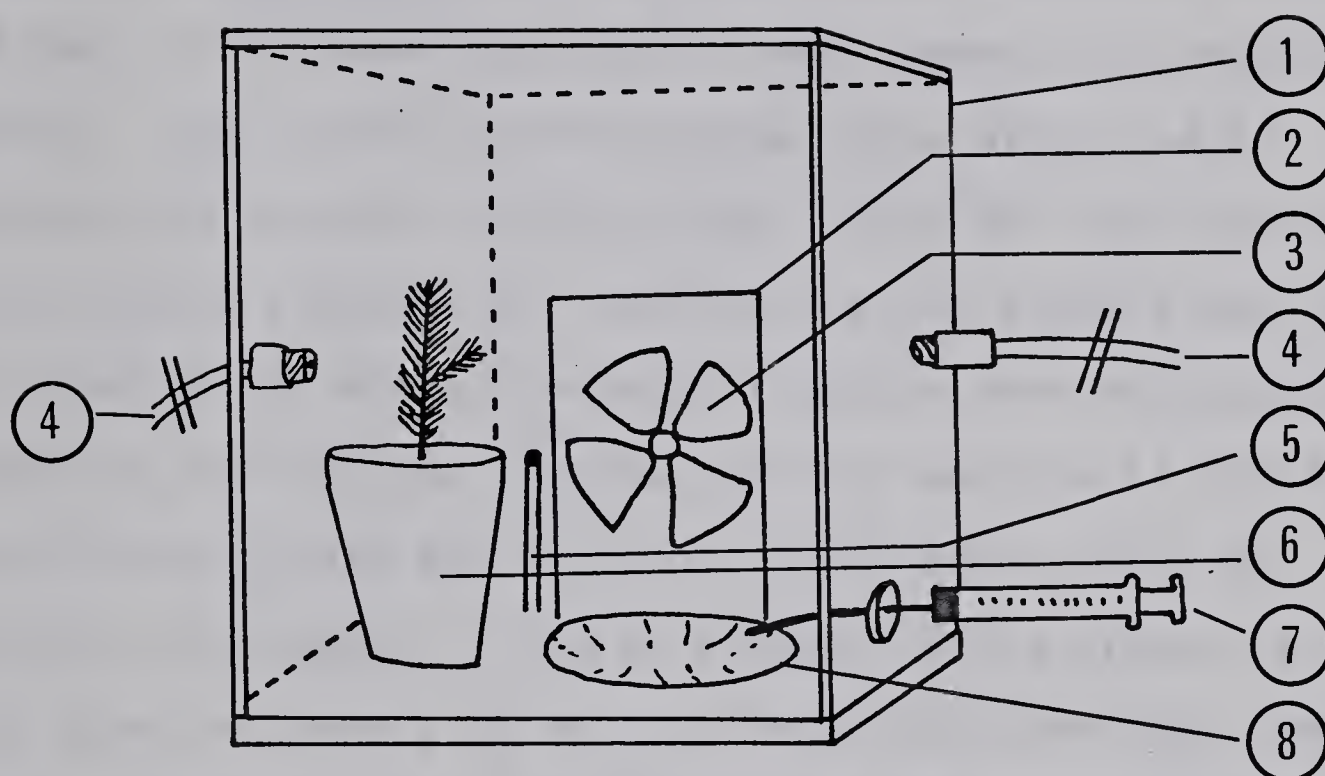


Figure 2. Assimilation chamber used in carbon-14 study of first- and second-year white spruce seedlings. 1) 8.3 litre chamber 2) shield to protect seedlings from fan blades 3) 3V DC fan 4) air intake/outlet for flushing chamber of residual carbon-14 5) thermistor 6) seedling 7) syringe 8) watchglass

photoassimilate all of the $^{14}\text{CO}_2$ (Lister et al. 1961, Ursino et al. 1968a).

Forty-eight hours after exposure, the plant was removed from the soil by careful washing in water. The shoot and roots were separated, weighed and then frozen in liquid nitrogen. Freezing killed the tissues and reduced respiration losses while the plant parts were oven dried for 2 days at 80C. Oven-dried parts were ground with mortar and pestle, and soluble carbohydrates twice extracted in boiling 80% ethanol (VV-1) (Ursino 1973) for one-half hour. A filtration process with scintered glass funnels was used to separate the ethanol-soluble fraction from the insoluble fraction. The soluble portion was then made up to 50 ml for second-year plants and 40 ml for first-year plants by addition of ethanol. A 0.5 ml aliquot of the extract was then pipetted into a 20 ml glass scintillation vial, and 17 ml of a dioxane based scintillation fluid (New England Nuclear, NEF 951) were added. The ^{14}C activity was assayed by liquid scintillation counting in a Nuclear-Chicago (ISOCAP/300) counter.

The ethanol-insoluble residue was dried and combusted using a modified Schoniger dry combustion technique (Wang and Willis 1965) (Figure 3). The evolved $^{14}\text{CO}_2$ was trapped in 50 to 70 ml of 2N NaOH, depending on the amount of tissue burned. The volume was made up to 100 ml with 2N NaOH and 0.5 ml aliquots were added to 15 ml of the scintillant. Radioactivity of the insoluble fraction was also assayed by

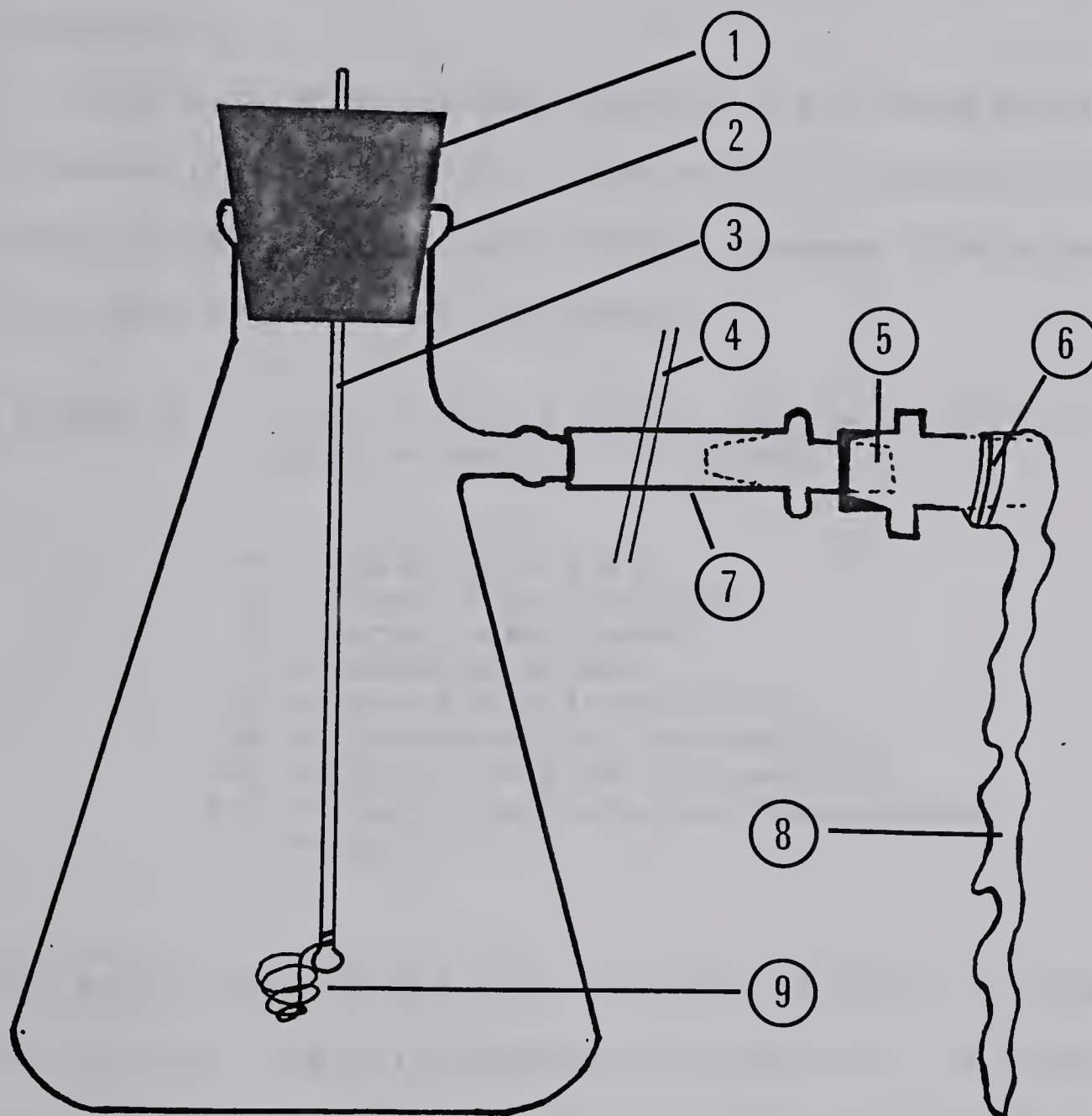


Figure 3. Modified Schoniger dry combustion flask used to release ethanol-insoluble ^{14}C 1) No. 6 rubber stopper 2) 1000 ml vacuum flask 3) glass rod 4) clamp 5) quick disconnect 6) wire 7) 3/8 in. tygon tubing 8) balloon 9) platinum wire

liquid scintillation counting. Counting efficiency was determined by an external standards ratio (ESR) method (Wang and Willis 1965), and the counts per minute (CPM) adjusted accordingly.

The data were analyzed using a 3 way analysis of variance (ANOVA) with an F test at $P \leq .05$ (Scheffe 1959). A linear least-squares curve fitting program (Daniel and Wood 1971) was used to test the model;

$$Y(ijkm) = M + A(i) + B(j) + C(k) + AB(ij) + AC(ik) + BC(jk) + ABC(ijk) + e(ijkm)$$

M = population mean
 A = time of year effect
 B = light level effect
 C = watering effect
 AB = time-light interaction
 AC = time-watering interaction
 BC = light-watering interaction
 ABC = time-light-watering interaction
 e = error

The model was used for each dependent variable: retention, distribution and partitioning of carbon-14. The model allowed determination of the individual effects of time (A), light (B), and watering (C), as well as the first- and second- order interactions. All data collected were in the form of percentages so they were transformed by the arcsine of the square root for analysis (Steel and Torrie 1960). Data for the first- and second-year seedlings were analyzed separately.

2. The Effect of Drying Soils on Survival

Forty-four, three inch pots, were filled with a "greenhouse mix" soil (3:2:2 loam, peat, sand) and another series of 44 pots were filled with sphagnum peatmoss (Sunshine brand). Each pot was seeded with enough seed to allow for a minimum of 15 germinants. The pots were kept in two controlled environment chambers programmed to simulate July temperatures and photoperiod (23C/12C, 17h). Each pot received enough water to maintain soils at field capacity. After the minimum number of one-month-old germinants was obtained, watering ceased. Daily Scholander pressure chamber (PMS Instrument Co.) readings (Figure 4) on a minimum of four seedlings in one pot were taken in order to determine the effect of drying soils on the xylem pressure potential of the seedlings. Seedlings remaining in the pot were returned to the growth chambers and were watered regularly. Survival was monitored for a period of three weeks. It was assumed that if seedlings survived for 3 weeks, any damage incurred by the drought did not hamper chances of further survival. Each day, another pot containing seedlings with similar xylem potentials was selected for each soil type. Bulk soil water content in the pot was determined gravimetrically.

The relationships between soil water content and xylem pressure potential and soil water content and survival were determined by standard regression analysis.



Figure 4. Scholander pressure chamber used to determine xylem pressure potentials.

B. Field Study

1. Site Description

The field study area was located in north-central Alberta, approximately 64 kilometres northeast of the town of Slave Lake (Figure 5). According to Rowe (1972) this site falls in the mixedwood section (B 18a) of the boreal forest region. The area is characterized by rolling morainic deposits on the uplands and smoother glacio-lacustrine deposits on the lowlands (Rowe 1972).

The study area was dominated by stands of mixed white spruce and trembling aspen (Populus tremuloides Michx.). The soil was a grey-wooded soil derived from a heavy, clay loam till. The depth of the LFH layer varied from 3 to 6 inches. The ground cover consisted primarily of feather mosses, scattered herbs and some shrubs. The herb layer was composed mainly of Aster sp., Equisetum sp., Cornus sp., some ferns and grasses. There was a considerable amount of dead and decaying wood, which appeared to offer a favorable site for germination of white spruce seed.

A portion of this area (Timber Licence S4-L20, block 212) was logged during the winter of 1975-76. Scarification with a modified toothed blade occurred during the same year.

Some micro- and meso-climatic data were collected and used to characterize the site (Table 2).

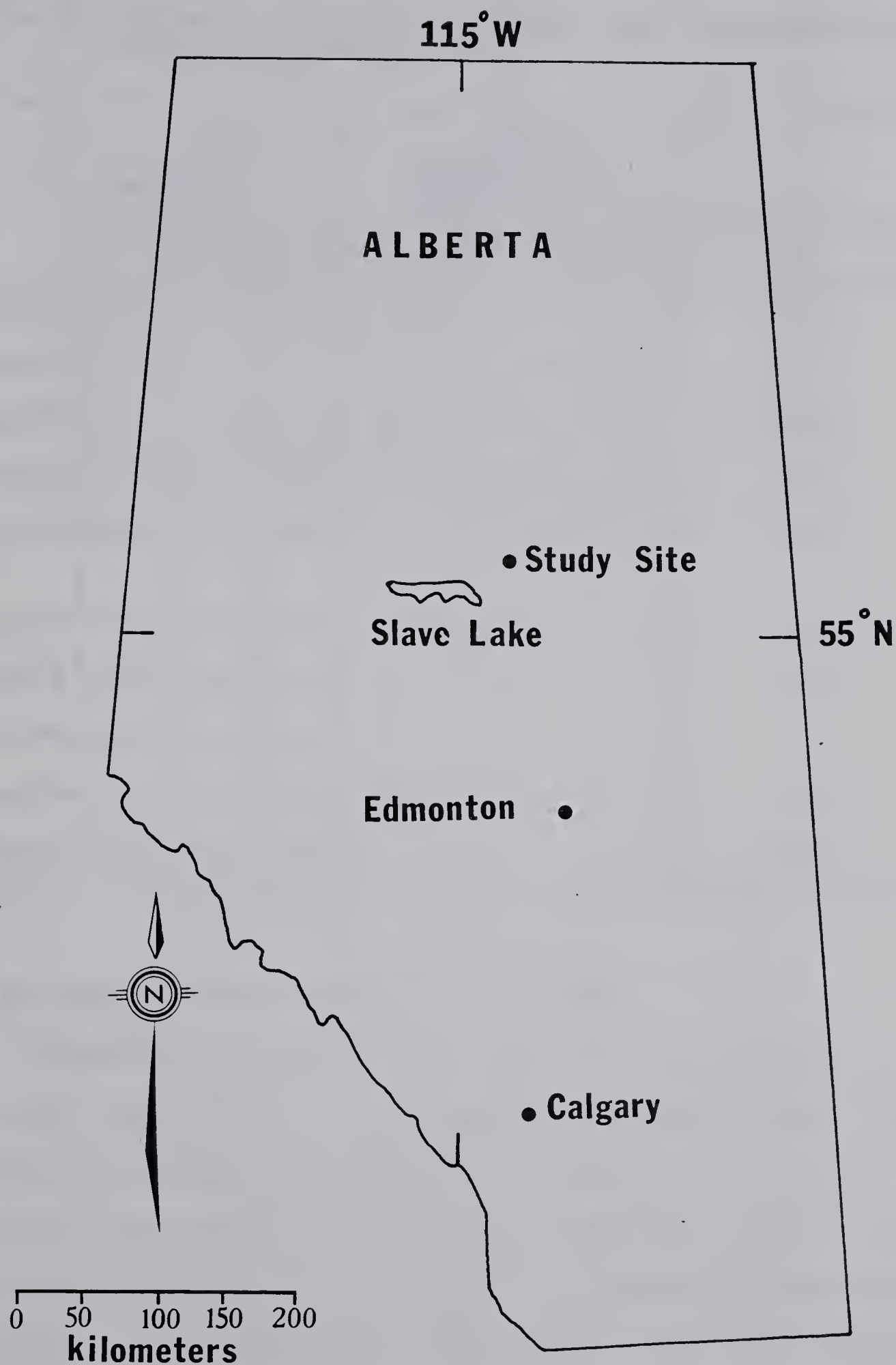


Figure 5. Map of Alberta showing the location of the field study area in relation to major population centres.

Table 2: Summary of monthly climatic data collected from the field study area.

Month	Mean Monthly Air Temperature °C			Mean Monthly Soil Temperature °C			Precipitation mm
	Max.	Min.	Mean	At 7cm	At 30cm	Mean	
May/77	17.0	5.4	11.2	8.7	1.7	5.2	103.2
Jun/77	19.8	8.9	14.4	15.3	9.4	12.4	76.9
Jul/77	19.4	8.5	14.0	13.4	10.8	12.1	114.6
Aug/77	17.1	6.1	11.6	13.4	11.2	12.3	81.3
Sep/77	13.4	4.7	9.1	10.7	9.4	10.0	70.8
May/78	14.9	3.7	9.3	9.8	4.4	7.1	78.6
Jun/78	20.8	8.0	14.7	--	--	--	90.0
Jul/78	21.2	9.7	15.5	--	--	--	27.9
Aug/78	18.9	8.4	13.7	13.8	10.0	11.9	69.3
Sep/78	13.4	5.6	9.5	--	--	--	130.8

2. Germination and Survival in the Field

Seventy-five 4.05 m² plots were located in both a clearcut (Figure 6) and in a mature mixedwood reserve stand (Figure 7) nearby. One-third were randomly selected as controls, one-third had the litter removed to mineral soil and the remaining one-third had the competing vegetation clipped. Twenty-five seeds were sown on each plot during the fall of 1976.

Germination and seedling survival were observed once each month from May to September during 1977 and 1978.



Figure 6. Clearcut area where 3 seedbed treatments were located.



Figure 7. Uncut area where 3 seedbed treatments were located.

During the first two visits in 1977, competing vegetation was removed from competition and mineral soil plots.

The effects of site (A), time of year (B) and seedbed type (C) on germination and survival were tested by a 3-way ANOVA of the model;

$$Y(ijkm) = M + A(i) + B(j) + C(k) + AB(ij) + AC(ik) + BC(jk) + ABC(ijk) + e(ijkm)$$

M = population mean
 A = site effect (clearcut vs. uncut)
 B = seedbed effect
 C = time of year effect
 AB = site-seedbed interaction
 AC = site-time interaction
 BC = seedbed-time interaction
 ABC = site-seedbed-time interaction
 e = error

III. RESULTS AND DISCUSSION

A. Laboratory Study

1. Retention of Carbon-14

Retention of recently photoassimilated carbon-14 can be influenced by a number of processes; photo-respiration and dark respiration (Lister et al. 1967), root exudation (Slankis et al. 1964), loss of plant parts, lateral movement of radioactivity from the phloem to the xylem (Roberts 1964), and during the transport of labelled solutes through the phloem (Roberts 1964). Factors related to experimental design or laboratory procedure can also influence apparent rates of retention. Such factors include the loss of plant parts during the removal of root systems from the soil and loss of radioactivity during preparation of tissue for extraction. Here, excessive washing of roots may result in the loss of water soluble components. Excessive dosages of radioactivity will cause internal damage, which may not be immediately apparent, to the sensitive seedlings (Ursino et al. 1968b). Finally, if insufficient time is allowed for all the carbon-14 to be assimilated, apparent retention will be low. This could be dependent on the size of the assimilation chamber used and the concentration of carbon dioxide within the chamber.

The rates of retention reported here were much lower than expected. Although absolute rates were low the results

are still valid in relative terms. Depending on the treatment, I recovered from 2.7 to 9.1 percent of the C-14 "fed" to first-year seedlings and from 3.2 to 20.6 percent from second-year seedlings. The rates of recovery reported by others include 30 percent after 6 days for red pine (Rangnekar and Forward 1969), 41.5 percent for jack pine (Pinus banksiana Lamb.) after 2 days (Balatinecz et al. 1966), 60 percent for white pine after 2 days (Ursino and Paul 1973) and 74 to 86 percent after two days for white spruce (Ursino 1973).

The reasons for such low values in this study are due partially to experimental errors. The assimilation chamber contained a fixed volume of 8.3 litres of air (330 ppm CO₂) plus 2.45 uCi of Na²¹⁴C¹⁸O₃ for a total of approximately 5 mg carbon dioxide (CO₂ + ¹⁴CO₂). Assuming maximum rates of CO₂ uptake at 320 uE m⁻²s⁻¹ light to be 16.7 mg g⁻¹ h⁻¹ (5 mg dm⁻² h⁻¹) (Higginbotham and Tear 1978), the first- and second-year seedlings could have taken up from 20 percent or 160 percent of the carbon, respectively. Thus, rates of retention for first-year seedlings were low because an insufficient amount of time was allowed for uptake of all the carbon-14 dioxide. White spruce probably utilizes the C-3 photosynthetic pathway, and these plants are usually sensitive to low CO₂ levels (Gaastra 1959). Photosynthetic rates for second-year seedlings were probably reduced because of low CO₂ levels, which probably developed within a one hour period. Photosynthetic rates were probably limited,

also, by low light levels in the growth chambers. A maximum of $320 \text{ uE m}^{-2}\text{s}^{-1}$ light intensity was attainable, representing approximately 20 percent full sunlight during mid-summer field conditions. Since all plants were actively growing during the period of this study, the rates of respiration might be expected to be high. Thus, the combination of experimental error and plant activity resulted in low rates of assimilation as reflected by low rates of retention.

There were significant differences ($P \leq .05$) in retention of ^{14}C due to time of year, light and watering for first-year seedlings (Table 3). Except for the light X watering interaction, first- and second- order interactions were also significant at $P \leq .05$. This indicates that there are significant differences in retention due to light and watering for each level of time, due to time and light for each level of watering etc..

Retention increased from May through August and declined in September (Figure 8). Seedlings grown under half-light conditions retained more ^{14}C than seedlings grown under full-light. The well-watered seedlings had higher rates of retention than those in the same light group which were watered less frequently. Similar trends were observed for total seedling growth (Figure 9).

There were significant differences ($P \leq .05$) in retention of ^{14}C in second-year seedlings due to time of year as well as the interactive effect of time and watering (Table 4).

Table 3: Analysis of variance of percent retention of carbon-14 in first-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.0503	45.73	$\leq .05$
Light	1	.0575	52.27	$\leq .05$
Watering	1	.0210	19.09	$\leq .05$
Time X Light	3	.0053	4.82	$\leq .05$
Time X Watering	3	.0134	12.18	$\leq .05$
Light X Watering	1	.0015	1.36	$> .05$
Time X Light X Watering	3	.0226	20.54	$\leq .05$
Error	48	.0011		
Total	63	.0056		

Table 4: Analysis of variance of percent retention of carbon-14 in second-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.0848	16.47	$\leq .05$
Light	1	.0023	<1	—
Watering	1	.0002	<1	—
Time X Light	3	.0093	1.82	$> .05$
Time X Watering	3	.0277	5.43	$\leq .05$
Light X Watering	1	.0143	2.80	$> .05$
Time X Light X Watering	3	.0034	<1	—
Error	42	.0051		
Total	47	.0118		

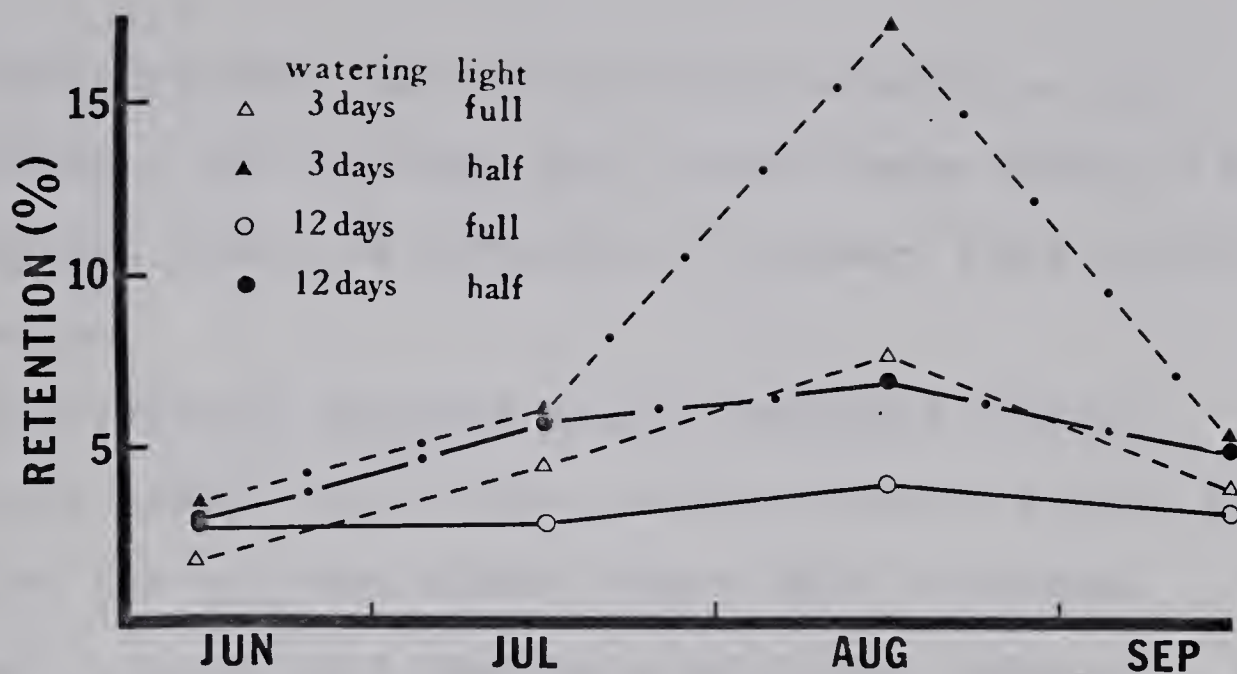


Figure 8. Seasonal changes in retention of carbon-14 in first-year white spruce seedlings.

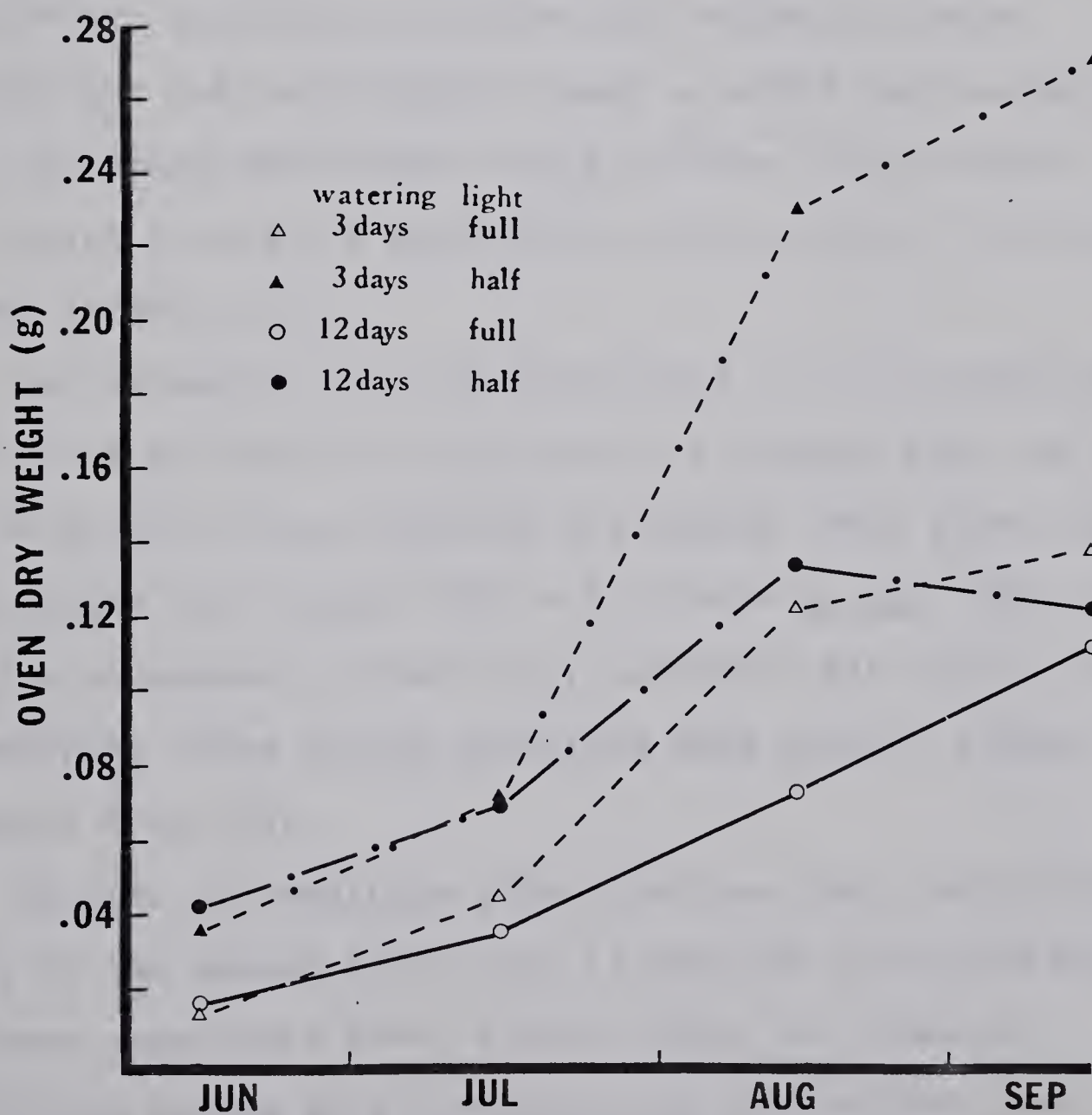


Figure 9. Seasonal changes in total growth of first-year white spruce seedlings.

This indicates that time of year and watering are not independent. Neither light nor watering were found to have a significant effect on retention of carbon-14 for second-year seedlings.

Two-year-old stressed plants exhibited bimodal retention peaks, one in June and the other in August (Figure 10). The non-stressed plants peaked only in August. Generally, half-light seedlings had higher rates of retention than full-light seedlings. Although watering was not found to have a significant effect on retention in second-year seedlings, both sets of stressed plants (full-light and half-light) showed a marked depression in July. Stressed full-light plants outgrew non-stressed full-light plants and half-light plants outgrew full-light plants (Figure 11).

Retention of recent photosynthate in tree seedlings has been found by others to increase to a maximum near the end of the growing season (Gordon and Larson 1968, Lister et al. 1967, Logan and Pollard 1971 and Shiroya et al. 1966). The results presented in this study indicate that first- and second-year white spruce seedlings show similar trends (Figures 8 and 10).

Growth, of seedlings older than one year, occurring early in the season arises out of the use of carbohydrate reserves (Kozlowski 1963, Sutton 1969). As climatic conditions become more favorable and leaf surface area increase, photosynthetic rates increase, and more of the

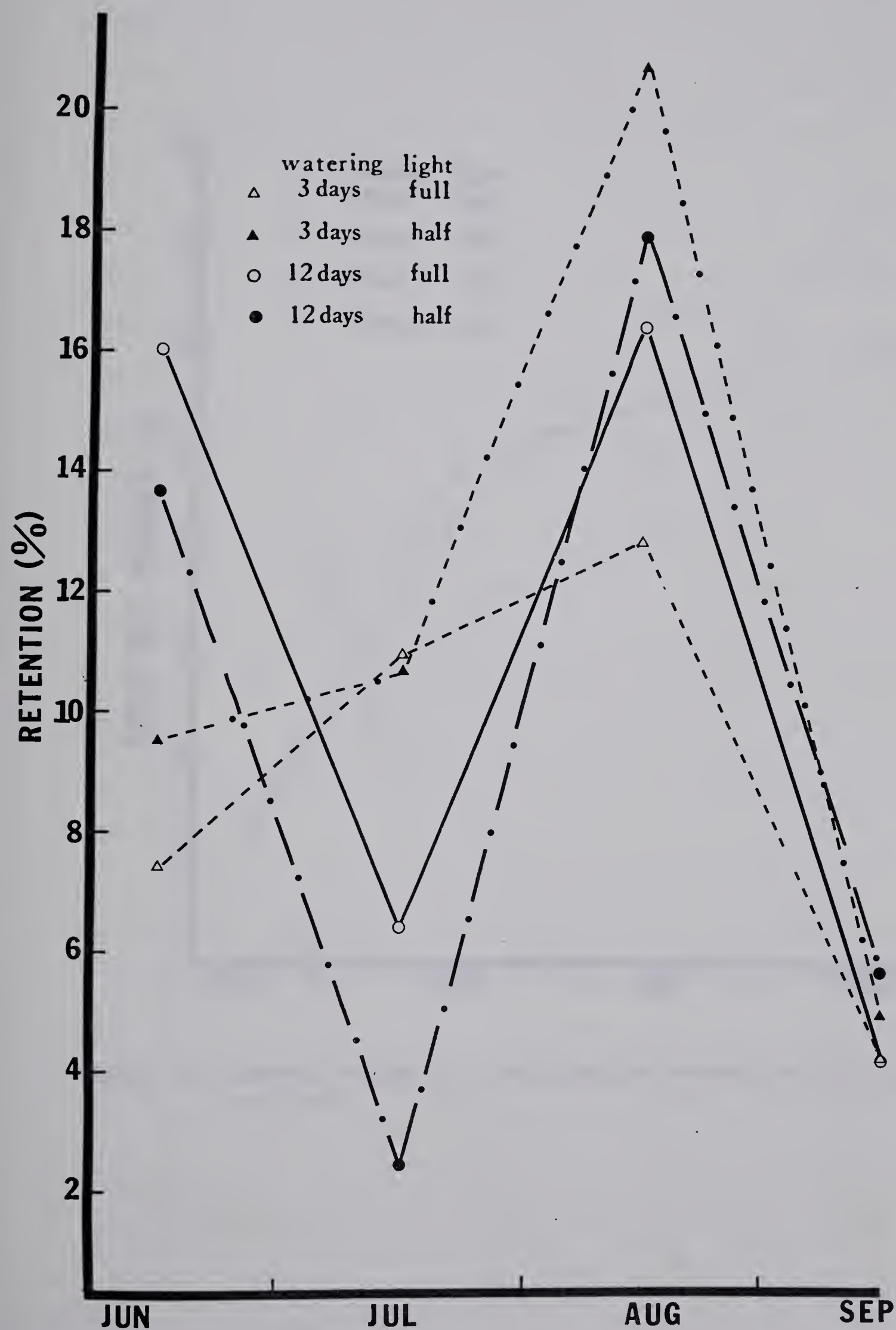


Figure 10. Seasonal changes in retention of carbon-14 in second-year white spruce seedlings.

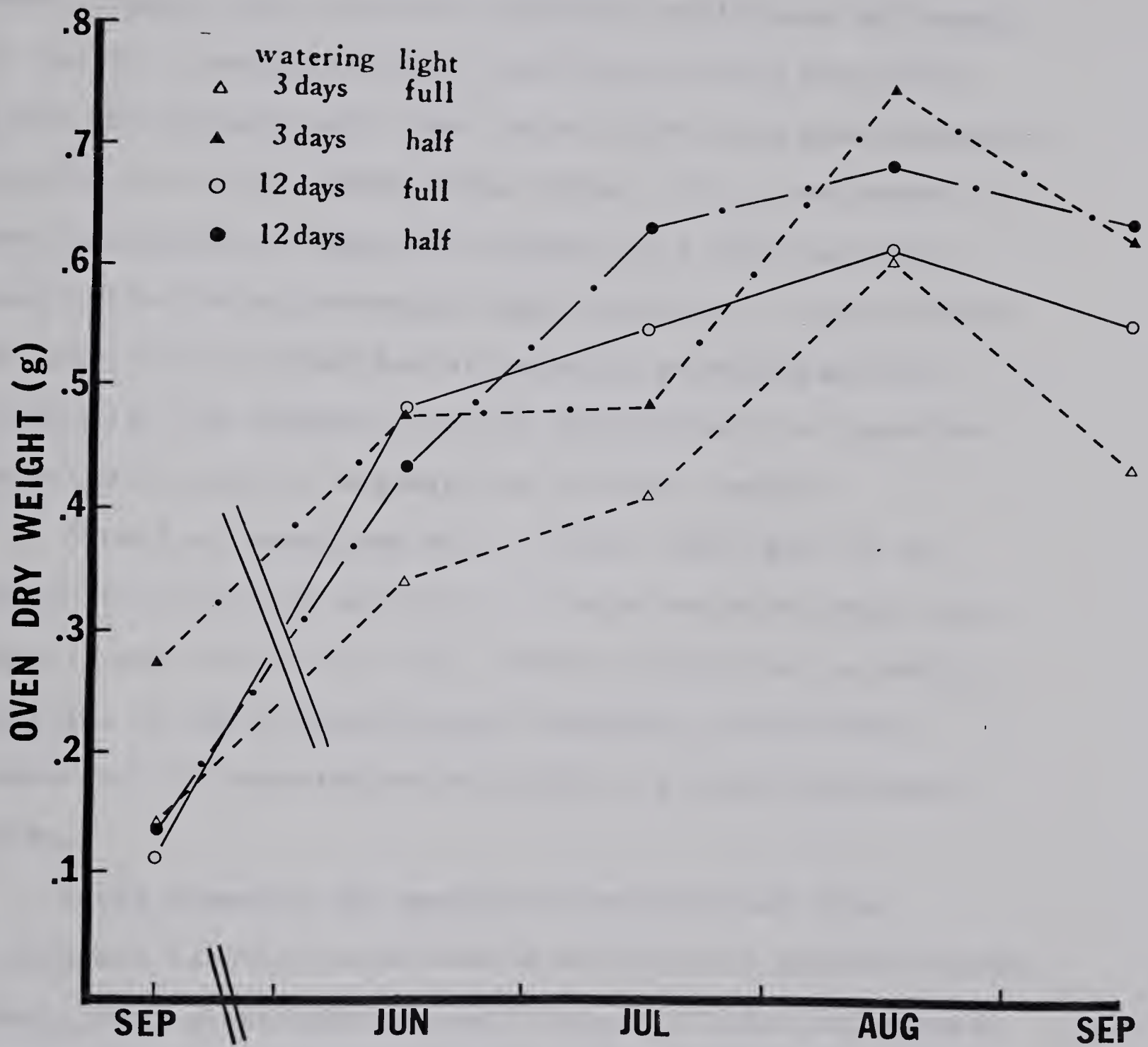


Figure 11. Seasonal changes in total growth of second-year white spruce seedlings.

recent assimilates are used for growth. By the end of June, most rapid shoot growth will have been completed (Hellum 1967). Thus, with increasing CO₂ uptake, rapid conversion of some of the carbohydrates and storage of the remainder, it seems logical that rates of retention would peak by August. It has been established that much root growth does take place during late fall, when shoot growth has been completed (Gordon and Larson 1968, 1970, Schier 1970). Low rates of photosynthesis in late fall coupled with high rates of respiration which accompany rapid growth will again result in low rates of retention of recently photoassimilated carbon-14. The remainder of the carbohydrate not used for growth will go into storage for the next season.

Growth of seedlings during their first-year is not dependent on stored carbohydrate reserves since only small amounts are stored in seeds. Growth, therefore, is solely a function of net photosynthesis. Seasonal patterns of retention are expected to be similar to those described above.

Light promotes the opening of stomata and thus influences the rate of diffusion of CO₂ into plants (Larcher 1969). Each plant species has a range of light intensities required for best growth. Growth is important to the early establishment of a seedling. Competition for light or water or both can be a major contributing factor to survival. Often a given species may adapt, to a point, to low light conditions. White spruce seedlings become established best

under shaded conditions (Day 1964, Place 1955). The data presented here would confirm this (Figures 8 and 9). First year seedlings showed highest rates of retention and best growth when grown under half-light conditions. Retention of ^{14}C for second-year seedlings seemed to be less affected by light (Figures 10 and 11).

Shiroya et al. (1966) found that the seasonal trend of apparent photosynthesis for two- or three-year-old white pine seedlings grown under low-light was similar to that of seedlings grown under high-light. The rates of apparent photosynthesis however, were lower. It would appear from the results presented here that first-, and to a lesser extent, second-year spruce seedling are better adapted to shade than are white pine seedlings.

The response of CO_2 gas exchange to water supply and water stress varies characteristically among species and ecotypes and depends strongly on age and soil moisture preconditioning (Larcher 1969). Photosynthesis is dependent on 3 classes of processes, (1) diffusive processes associated with the supply of CO_2 at the sites of photosynthesis, (2) photochemical processes associated with the utilization of light energy and (3) chemical processes associated with chemical reduction of CO_2 (Slatyer 1967). All of these processes can be affected by water stress.

Brix (1962) found that rates of net photosynthesis in loblolly pine (Pinus taeda L.) seedlings decreased to zero with increasing water stress. Respiration rates were found

to first decrease to 60% of the rates when soils were at field capacity then increase dramatically, to 145%, before decreasing again.

The results of this study showed that retention of ^{14}C of first-year white spruce seedlings was influenced by soil moisture status. Within each light group the seedlings grown under low soil moisture retained less ^{14}C than those in the 3-day watering group. Low rates of retention in these plants may have been due to increased stomatal resistances or increased rates of respiration or both. The differences in retention due to water stress were accentuated in August when growth (biomass) was peaking and water requirements were greatest.

Second-year seedlings showed interesting differences in seasonal trends of retention due to stress preconditioning. The bimodal pattern showed that in July a drastic drop in retention occurred for the 12-day seedlings. This coincided with a burst of growth for stressed plants during July (Figure 11). Data to be presented later indicated that much of retained ^{14}C went into structure and that root growth was emphasized. Growth during this period of stress was expected to be accompanied by increased respiration rates and subsequent low retention of recent photosynthate.

The effect that watering had on growth of second-year seedlings (Figure 11) was difficult to interpret. Within each light group the 12-day watered plants outgrew the 3-day watered plants. The demands for water are expected to be

greater for older seedlings. Thus a lack of water should have a greater affect on physiological processes for these plants. Possibly seedlings become more efficient at closing their stomata during periods of prolonged stress once they have been preconditioned to stress. Also, watering the seedlings every three days may have left the soil too wet and competition for oxygen may have been a limiting factor for growth.

2. Distribution of Carbon-14

Factors such as mycorrhizae (Nelson 1964), mineral nutrition (Nelson 1964), growth stage (Schier 1970), light intensity (Shiroya et al. 1966) and soil water stress (Roberts 1964) can affect the pattern of distribution of carbon-14 to the roots of seedlings.

The amount of carbon-14 in roots did not vary significantly with time, light or watering (Table 5) for first-year seedlings. There was, however, a significant difference ($P \leq .05$) for the second-order interaction, time X light X watering. This implies that the three factors act together in their influence on the redistribution of carbon-14 in first-year white spruce seedlings.

At no time during the study period was more than 34% of retained carbon-14 translocated to the roots. By June the amount of ^{14}C translocated to the roots had probably declined (Figure 12). The data also indicate that by September the amount going to the roots was increasing.

Table 5: Analysis of variance of percent carbon-14 in roots of first-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.0135	1.99	>.05
Light	1	.0205	3.01	>.05
Watering	1	.0206	3.91	>.05
Time X Light	3	.0007	<1	—
Time X Watering	3	.0067	<1	—
Light X Watering	1	.0006	<1	—
Time X Light X Watering	3	.0192	2.82	≤.05
Error	48	.0068		
Total	63	.0075		

Within each watering regime, first-year, full-light seedlings translocated more ^{14}C to roots than half-light seedlings. However, half-light seedlings showed greater rates of root growth than full-light seedlings (Figure 13). Possibly more of the translocated ^{14}C went into root growth rather than into storage, resulting in more biomass production. The 12-day watered seedlings translocated more ^{14}C to the roots than 3-day watered seedlings. The growth data showed a similar trend. It is apparent that stress preconditioning increased root metabolic activity thereby increasing the "pull" of photosynthates to the roots.

Distribution of ^{14}C between the shoot and root of the

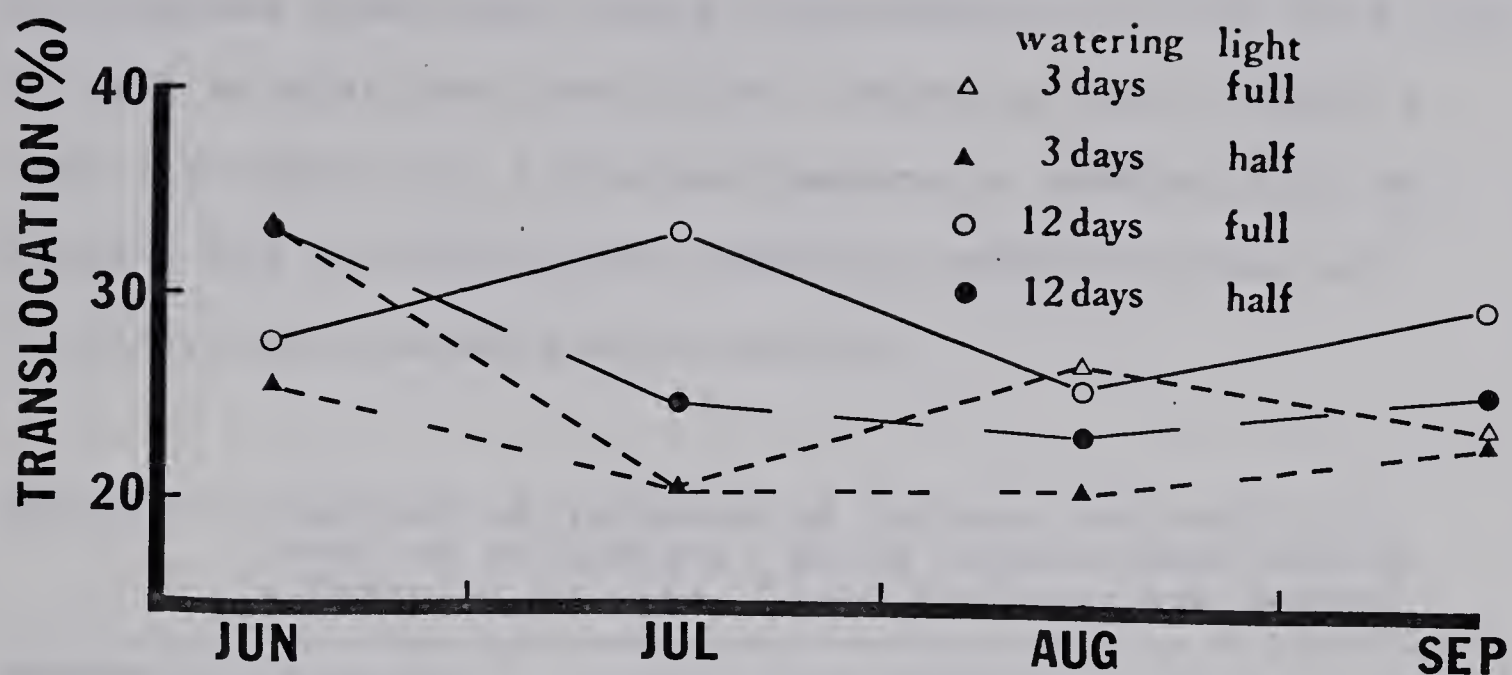


Figure 12. Seasonal changes in translocation of carbon-14 to roots of first-year white spruce seedlings.

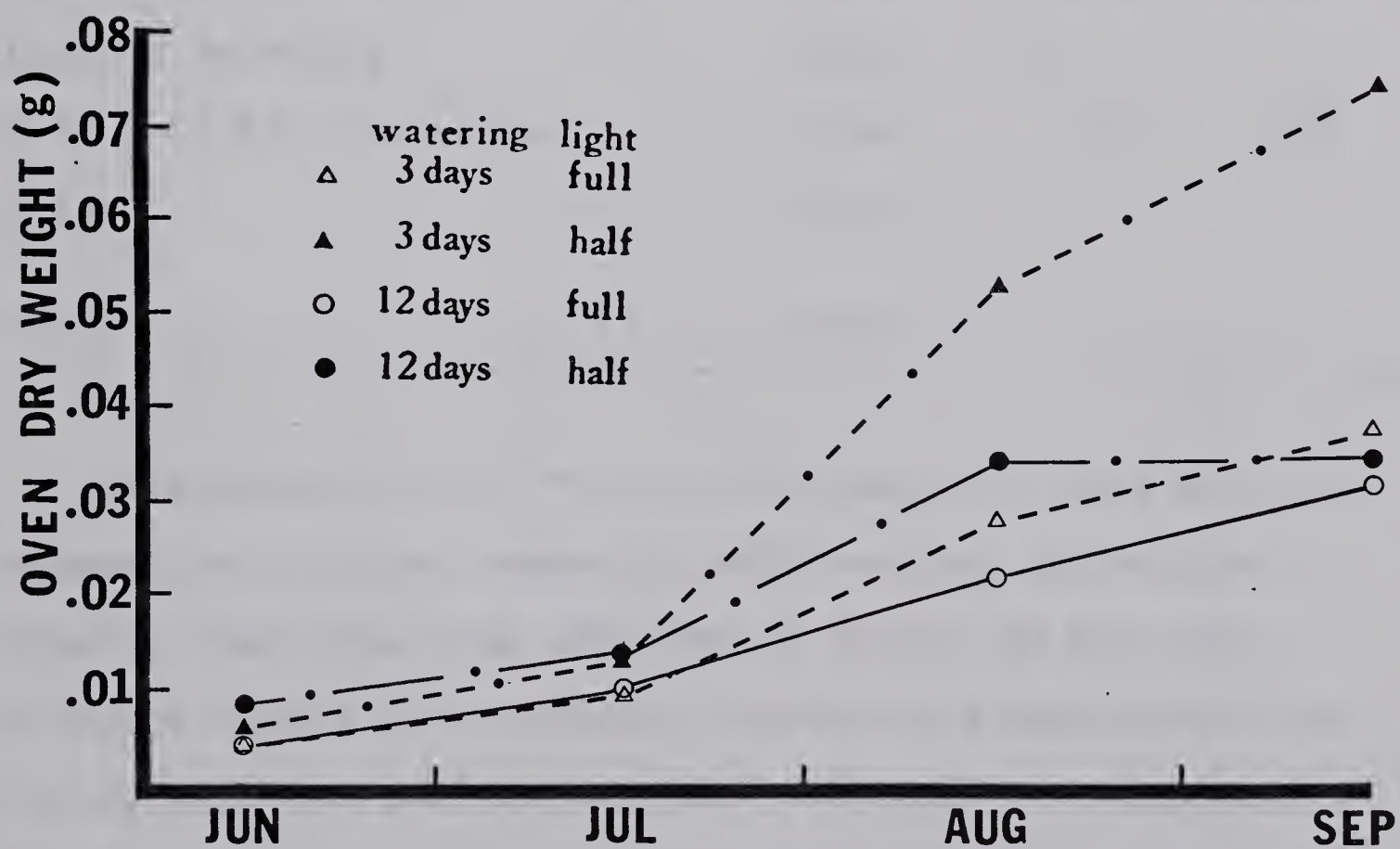


Figure 13. Seasonal changes in root growth of first-year white spruce seedlings.

second-year seedlings varied significantly ($P \leq .05$) with time as well as with the interactive effect of time X light X watering (Table 6). All other factors or combinations of factors had no significant effect on redistribution of recently photoassimilated carbon-14.

Table 6: Analysis of variance of percent carbon-14 in roots of second-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.0382	4.34	$\leq .05$
Light	1	.0075	<1	—
Watering	1	.0018	<1	—
Time X Light	3	.0025	<1	—
Time X Watering	3	.0243	2.76	$> .05$
Light X Watering	1	.0024	<1	—
Time X Light X Watering	3	.0284	3.23	$\leq .05$
Error	32	.0088		
Total	47	.0122		

Translocation of ^{14}C to roots peaked in July for all second-year plants, except in well-watered, half-light plants, where the peak occurred in August (Figure 14). Stressed plants had a bimodal pattern of translocation to roots, with one peak in July and the other in September or later. Non-stressed plants had peak periods of translocation in July or August. It is clear that a great deal of root

growth occurred between September of one year and June of the next (Figure 15). This is probably true under field conditions providing soil temperatures are above freezing. Generally, roots of half-light plants outgrew roots of full-light plants within each watering regime.

The amount of ^{14}C translocated to roots has been found to vary from study to study, from 20 percent in jack pine after 3 days (Balatinecz et al. 1966), to 50 percent in white pine after 2 days (Ursino and Paul 1973) and in red pine after 6 days (Rangnekar and Forward 1969), to 30 and 45 percent in white spruce after 2 days (Ursino 1973). The results presented for white spruce indicate that from 20 to 35% and 20 to 55% of recently photoassimilated ^{14}C is translocated to roots of first- and second-year seedlings, respectively.

Seasonal trends in the redistribution of ^{14}C in pine seedlings have received a great deal of attention. Both white and red pine increased translocation to roots at the end of the growing season (Gordon and Larson 1968, 1970, Schier 1970, Ursino et al. 1968a). White pine has been found to exhibit a bimodal pattern of translocation to roots with peaks in the spring and autumn (Lister et al. 1967, Nelson 1964, Shiroya et al. 1962a, 1966). According to Kramer and Kozlowski (1960) the bimodal peaks may be a result of spring and fall periods of root growth often observed in temperate climates. During spring, serious competition for recently assimilated ^{14}C arises when developing buds have high

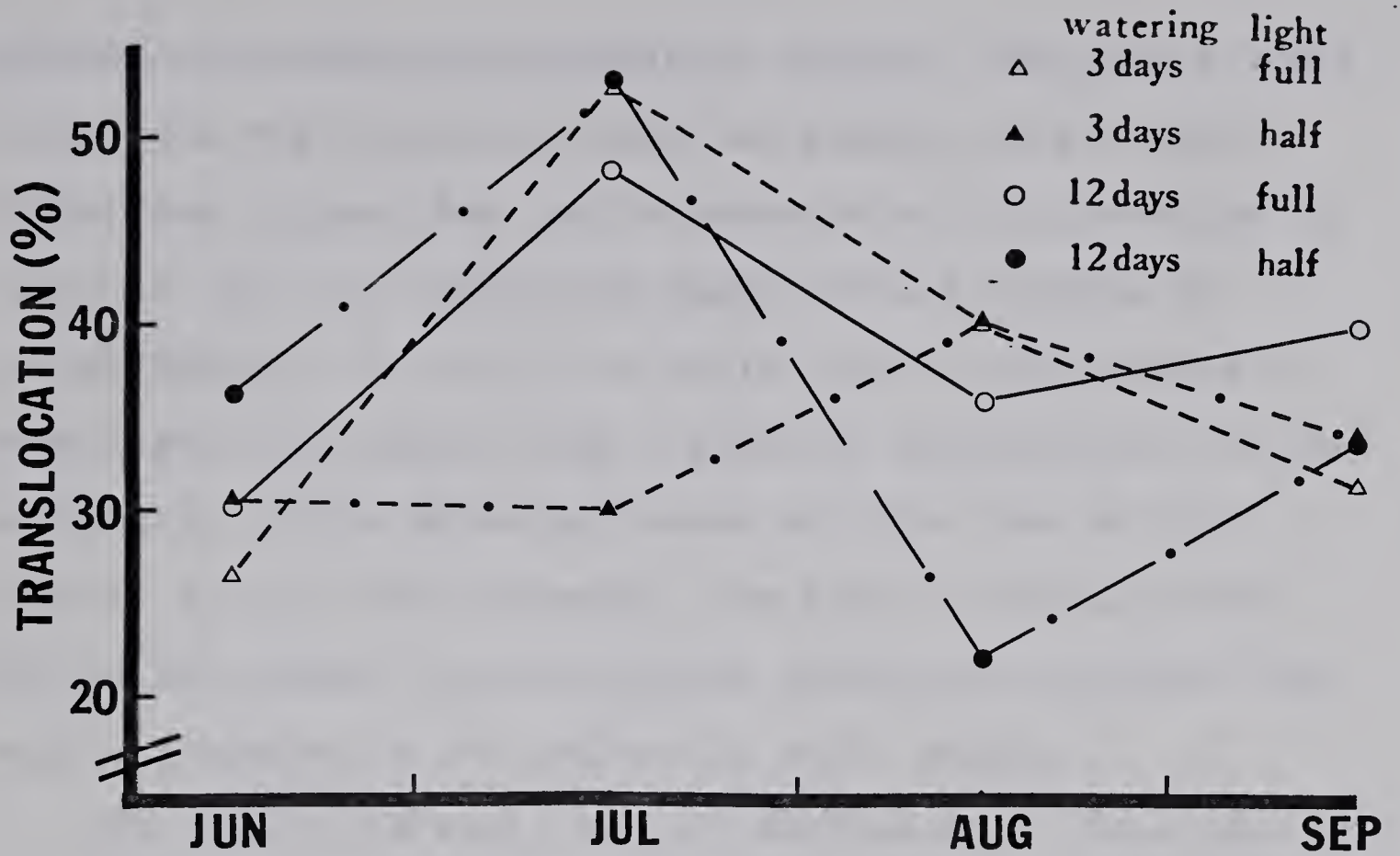


Figure 14. Seasonal changes in translocation of carbon-14 to roots of second-year white spruce seedlings.

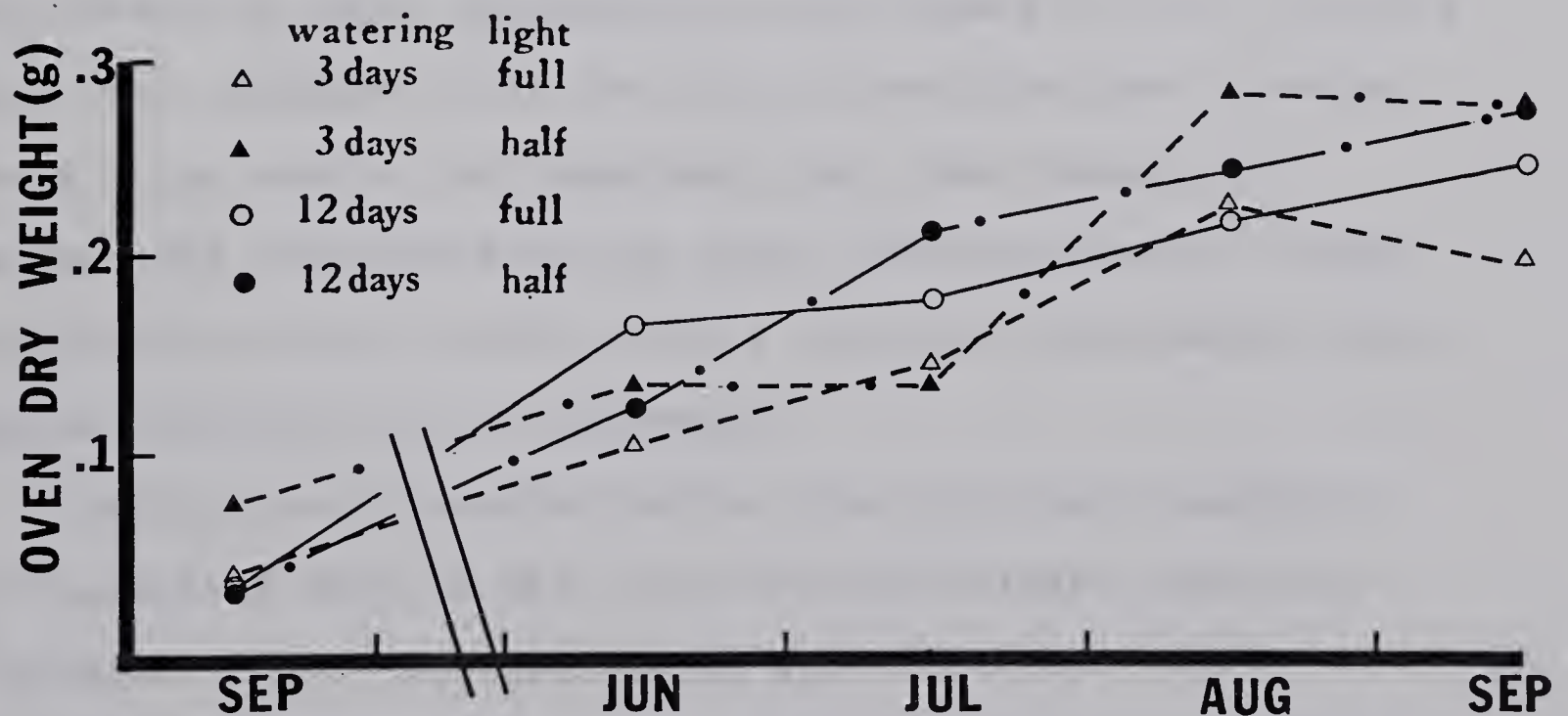


Figure 15. Seasonal changes in root growth of second-year white spruce seedlings.

demands for current photosynthate (Ziemer 1971). This would agree with the hypothesis given by Kramer and Kozlowski (1960) and account for the de-emphasis of translocation to roots in the late spring and summer. The low rates of redistribution of ^{14}C in the early part of the growing season may also result from a block or discontinuity in the conducting system which may occur at this time of year (Lister et al. 1967). However, the peak in translocation during mid-summer for second-year seedlings indicates that such a blockage is not evident in white spruce.

The period of study was not sufficient to determine if bimodal trends of translocation to roots exist for first- and second- year white spruce. The mid-summer peak in translocation in second-year seedlings does confuse the issue. This peak might correspond to a period of accelerated root growth, as suggested by data collected on partitioning of carbon-14. Data collected on root growth did not indicate any such increased root activity. Growth data are based on oven dried weights and represent both the storage and structural components of the plant. Thus the use of stored carbohydrates for current growth would not necessarily show up as increased growth (biomass).

Within each watering regime the full-light seedlings translocated more to the roots than half-light seedlings (Figures 12 and 14). Shiroya et al. (1962a and 1966) obtained similar results with eastern white pine seedlings. Perhaps roots of full-light seedlings have use for greater

amounts of recent photoassimilates. Data presented in the next section will show that more of this recent photoassimilate remained in the nonstructural form (i.e. in the form of sugars or starch probably for storage). Conversely, half-light seedlings put more emphasis on shoot growth. This is a reflection of the differences in competition between sinks for recently formed carbohydrates.

Little work has been carried out to determine the effect of soil moisture on translocation of carbon-14 assimilated by plants. Lister et al. (1967) found that soil moisture made no difference in rates of translocation to roots for white pine seedlings. This is contrary to what was expected. Soil water stress reduces photosynthesis (Larcher 1969) and thus indirectly reduces the amount of recent photoassimilate available for redistribution. Also, the theory of mass movement of solutes in the phloem of tree seedlings suggests that the level of metabolic activity in roots affects the degree of "pull" of assimilates to the roots. Therefore water stressed plants should exhibit reduced rates of translocation of carbohydrates to the roots. Roberts (1964) found that water stress in yellow poplar (Liriodendron tulipifera L.) caused a shift to upward movement of ^{14}C , probably due to strong competition by apical meristems for the products of photosynthesis.

If seedlings are grown under conditions of low soil moisture throughout a growing season, it might be reasonable to assume that continuously low levels of assimilates would

be translocated to roots for reasons described above. Conversely, seedlings grown under optimal or near optimal conditions might be expected to show continuous root growth and translocation of photosynthate to roots throughout the entire growing season. The results presented here do not comply with the hypothesis proposed above. The data indicate that soil water stress caused an increase in translocation to the roots for first-year seedlings. By the second year the response of translocation to stress became more variable.

3. Partitioning of Carbon-14

Schier (1970) found that the ^{14}C in the sugar fraction in red pine remained about 3 to 4 percent at all times of the year. This is probably related to the metabolic function of sugars in plants. He believed that because sugars remain an important metabolic pool in the redistribution of ^{14}C , the level of ^{14}C probably became constant when inflow and outflow were balanced.

There is evidence that the incorporation of recent photosynthate into structural components is rapid. Ursino and Paul (1973) found that 10% of the recovered carbon-14 found in the ethanol-insoluble form in white pine after 1.5 hours of exposure. After 1 hour, between 18 and 45 percent of the recovered ^{14}C from white spruce in this study was found in the ethanol-insoluble form.

The amount of recently assimilated carbon-14 channelled

into plant structures has been found to vary: 33 percent 6 days after uptake for red pine (Rangnekar and Forward 1969), 40% after 2 days for white pine (Ursino and Paul 1973), and 50% after 2 days for jack pine and white spruce (Balatinecz et al. 1966 and Ursino 1973), and from 18.0 to 72.5 percent after 2 days for white spruce seedlings depending on the time of year, according to my study.

Partitioning of recently assimilated carbon-14 in first year seedlings was found to vary significantly ($P \leq .05$) with time of year and due to the interactive effect of time X light X watering (Table 7). There was an obvious decline in the percent insoluble fraction with time (Figure 16). This accumulation of storage products will probably be used later by the plant to substitute for or supplement current photosynthate production.

Plants grown under full-light and watered every 12-days had consistently higher percentages of ^{14}C in the insoluble fraction than plants grown under full-light and watered every 3-days. This indicates that in these plants more emphasis was placed on structural growth rather than storage. Plants grown under half-light and watered every 12-days had more ^{14}C in the insoluble fraction in June and September only than half-light 3-day watered plants.

Partitioning of carbon-14 into ethanol-soluble and -insoluble fractions for second-year seedlings varied significantly ($P \leq .05$) with time and light (Table 8). There were also significant differences due to the interactive

Table 7: Analysis of variance of percent carbon-14 in insoluble forms in first-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.4226	33.54	$\leq .05$
Light	1	.0056	<1	—
Watering	1	.0133	1.06	—
Time X Light	3	.0253	2.01	$> .05$
Time X Watering	3	.0203	1.61	$> .05$
Light X Watering	1	.0007	<1	—
Time X Light X Watering	3	.0615	4.88	$\leq .05$
Error	48	.0126		
Total	63	.0330		

Table 8: Analysis of variance of percent carbon-14 in insoluble forms in second-year white spruce seedlings as a function of time, light and watering regime.

Source of Variance	DF	Mean Square	F	P
Time of year	3	.1637	22.74	$\leq .05$
Light	1	.0702	9.75	$\leq .05$
Watering	1	.0148	2.06	$> .05$
Time X Light	3	.0120	1.67	$> .05$
Time X Watering	3	.0288	4.00	$\leq .05$
Light X Watering	1	.0670	9.31	$\leq .05$
Time X Light X Watering	3	.0192	2.67	$> .05$
Error	32	.0072		
Total	47	.0224		

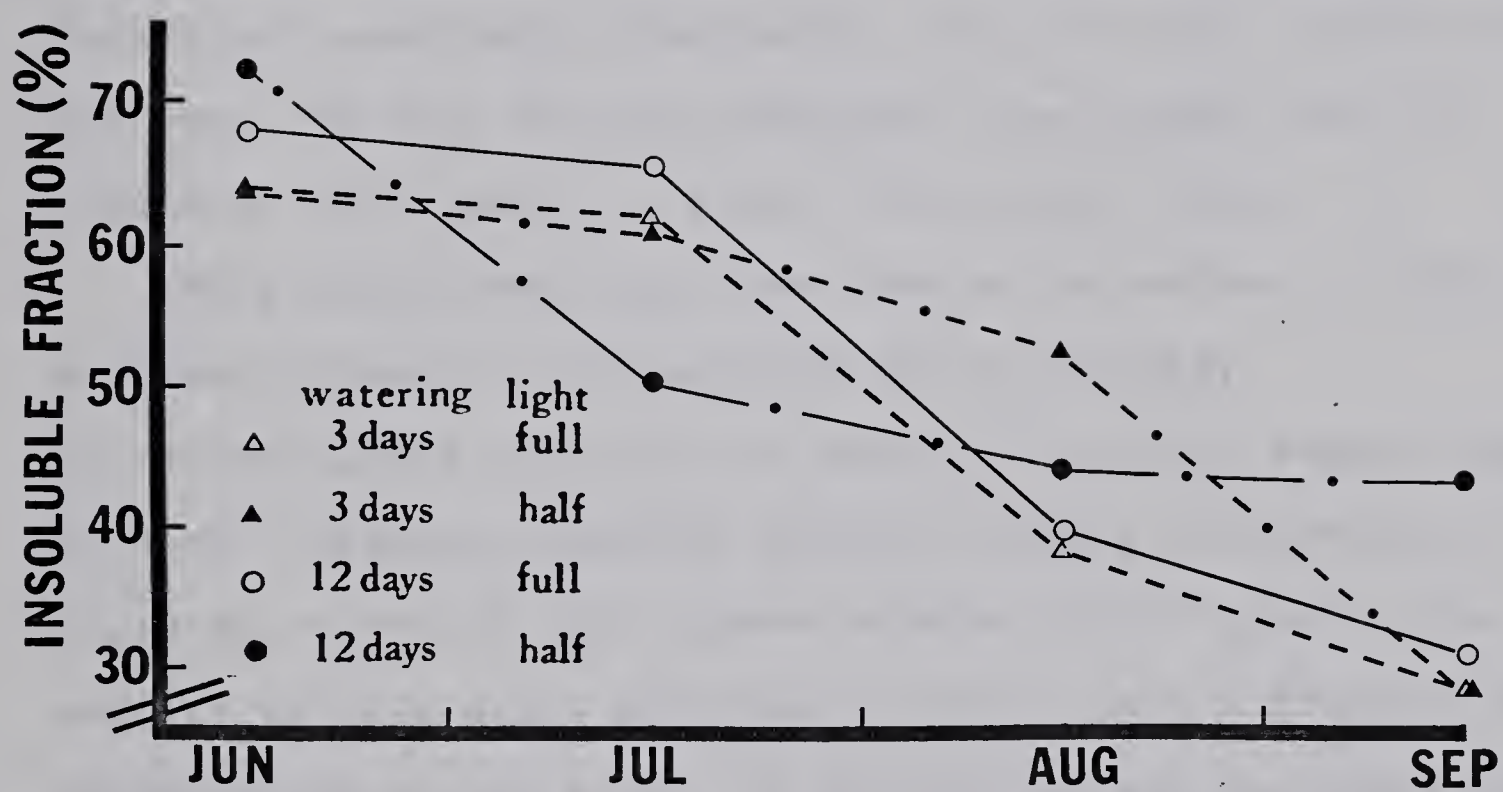


Figure 16. Seasonal changes in partitioning of carbon-14 to insoluble forms in first-year white spruce seedlings.

effects of time X watering and light X watering.

There was as much as a two-fold increase of ^{14}C channelled into structural components in July (Figure 17), but by September more ^{14}C (74 to 82 percent) went into storage. Generally, seedlings grown under half-light conditions had more of the recently photoassimilated carbon-14 channelled into structural materials. This agrees with the growth data for second-year seedlings (Figure 11). Full-light seedlings, grown under water stress, appeared to put more ^{14}C into storage throughout the season than did seedlings which were not grown under water stress.

Very little work has been done on the effect of light or water stress on the partitioning of recently photoassimilated carbon-14 in plants. One might expect that if light influenced growth, greater amounts of insoluble ^{14}C would be recovered from plants showing better growth. The results of this study indicate no statistical difference in partitioning in the first- or second-year due to light, even though there were differences in growth due to light.

Water stress, on its own, had no clear effect on partitioning of ^{14}C in first-year seedlings but resulted in a general reduction in production of carbohydrates. Two-year-old water-stressed plants put more emphasis on storage than did the non-stressed plants. These stressed plants, therefore, build up carbohydrate reserves which during more favorable climatic/edaphic conditions, will allow them to show a burst of growth using reserve

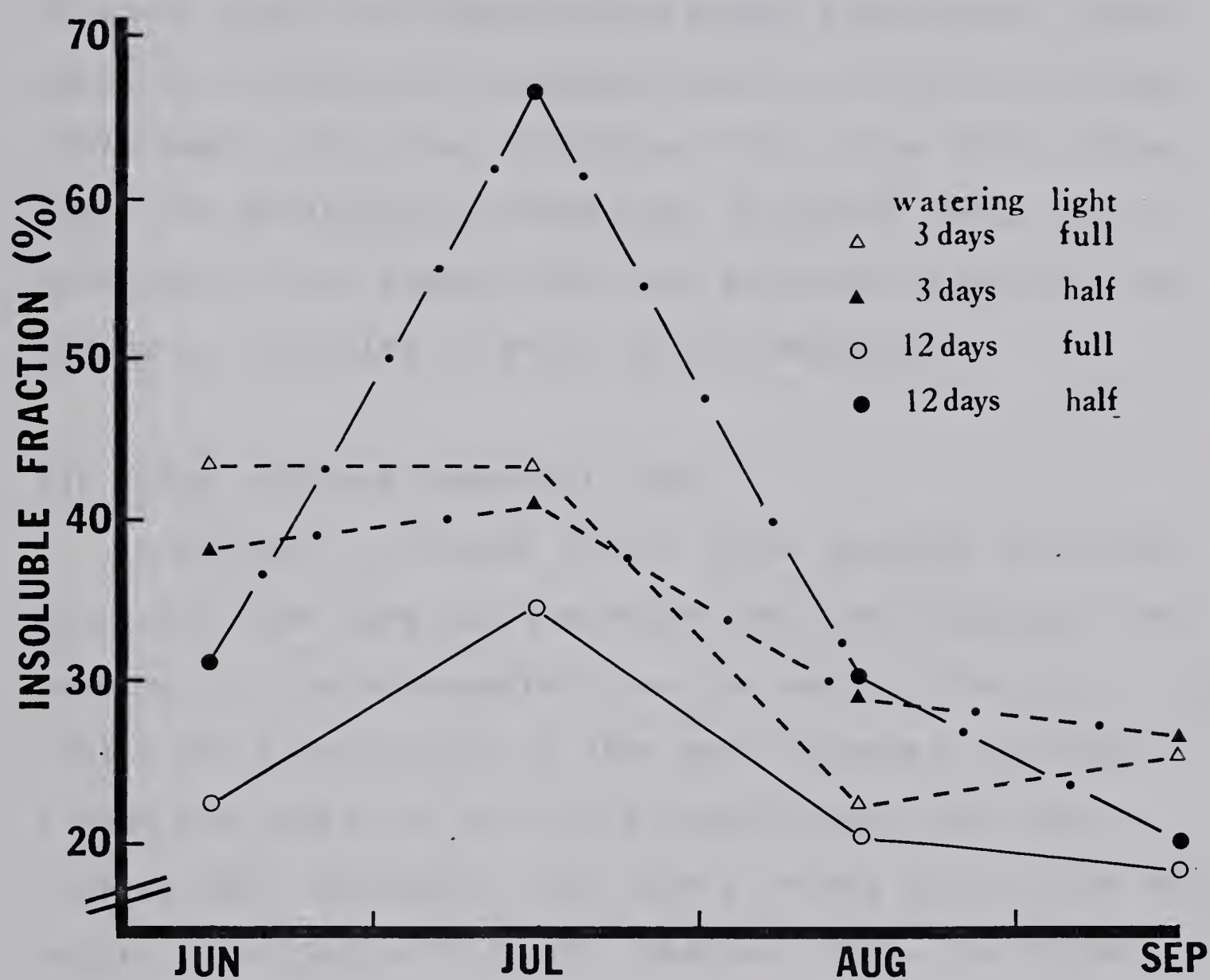


Figure 17. Seasonal changes in partitioning of carbon-14 to insoluble forms in second-year white spruce seedlings.

carbohydrates.

4. The Effect of Drying Soils on Survival

Many factors have been suggested to explain the lack of success of white spruce regeneration in Canada. They include drought, competing vegetation, seedbed receptivity, heat, rodents, insects and diseases. However, drought (Ackerman 1957, Bedell 1948, Day 1964, Eis 1965, Place 1955, Sutton 1969) and unsuitable seedbed type (Crossley 1949, Hellum 1972, Lees 1964, Sutton 1969) are believed to be the major causes of mortality in white spruce seedlings.

(1) Xylem Pressure Potential (XPP)

According to Slatyer (1967) xylem pressure potential decreases from dawn until mid-day and then increases toward evening. It can be expected that the matric potential of the soil = XPP of the plant at dawn when internal gradients within the plant and soil have equilibrated overnight. Predawn XPP, therefore, will show a strong correlation with matric potential of the soil (Slatyer 1967). The xylem potential measurements in this study were predawn observations, and therefore should represent maximum daily XPP and soil matric potential.

Time since last watering was found to have a significant effect ($P \leq .05$) on XPP (Table 9). There were also significant differences ($P \leq .05$) between soil types.

Table 9: Analysis of covariance for the effect of drying soils on xylem pressure potential of one-month-old white spruce grown on 2 soils.

Source of Variation	DF	Mean Square	F	P
Days	1	18.844	509.390	$\leq .05$
Soil	1	1.914	51.746	$\leq .05$
Explained	2	9.512	257.137	$\leq .05$
Residual	147	0.037		
Total	149	0.164		

Mineral soil dried out faster than peatmoss (Figure 18). This was also reflected in the more rapid decline in XPP of seedlings grown on mineral soil. The rate of decline of XPP accelerated with soil matric potentials exceeding -0.7 Mega Pascals (MPa) for mineral soil whereas an accelerated decline for the peatmoss began at -1.5 MPa. In general, the rapid rates of decline of XPP appeared to commence when soil water content was approaching a minimum of 5% and 50% for mineral soil and peatmoss (Figures 18A and 18B).

Xylem pressure potentials can be maintained at about -1.3 MPa for thirty one days without watering for both mineral soil and peatmoss (Figure 19) in three-month-old white spruce seedlings grown in 10 cm-deep soil trays.¹ The rooting medium did not appear to influence the rate of

¹Tear, E.C. 1978. Unpublished data on file at the University of Alberta, Edmonton.

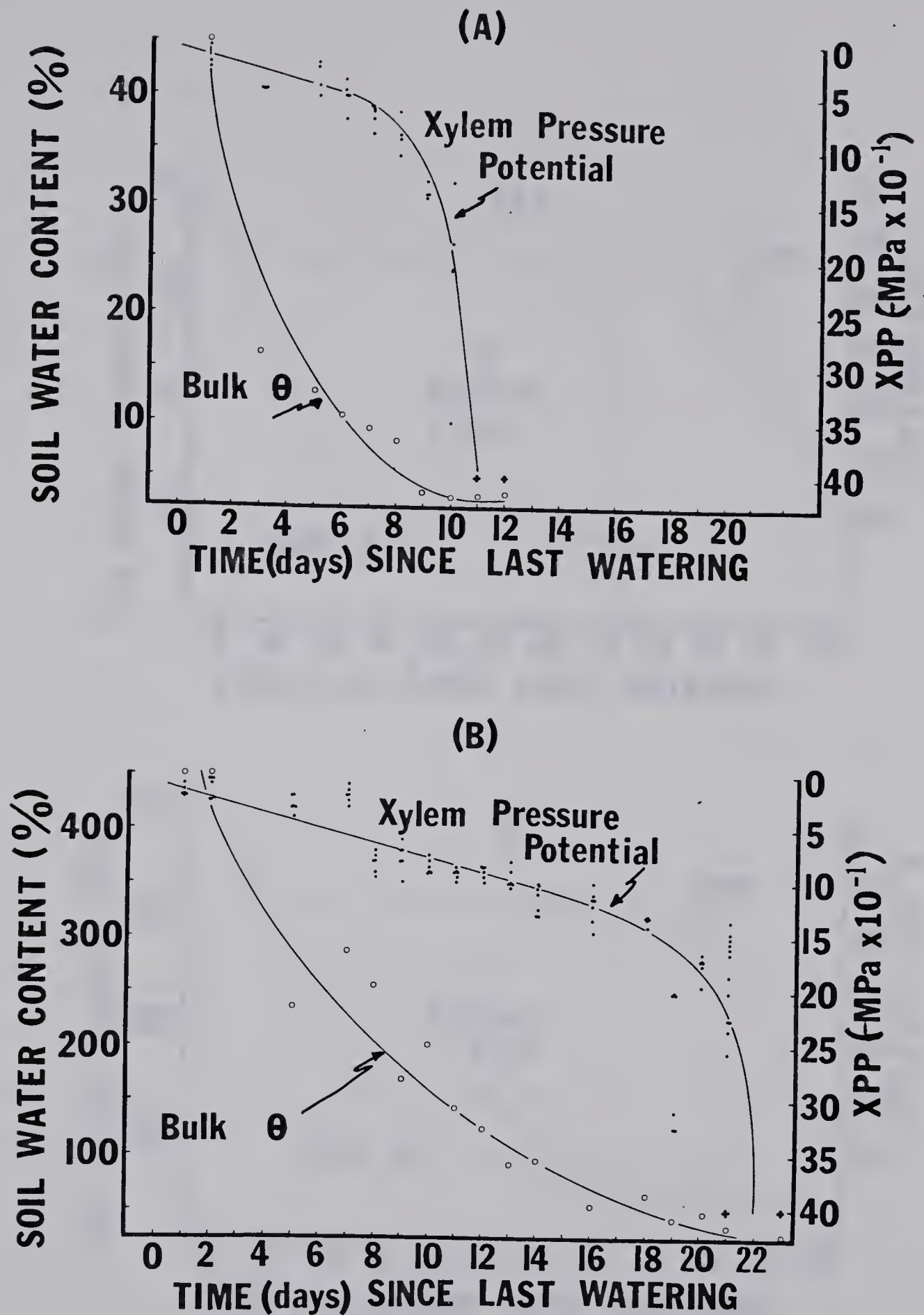


Figure 18. Relationships between time since last watering and xylem pressure potential (XPP) of one-month-old white spruce seedlings and between time since last watering and soil water content (θ) of a "greenhouse mix" (A) and a peatmoss (B).

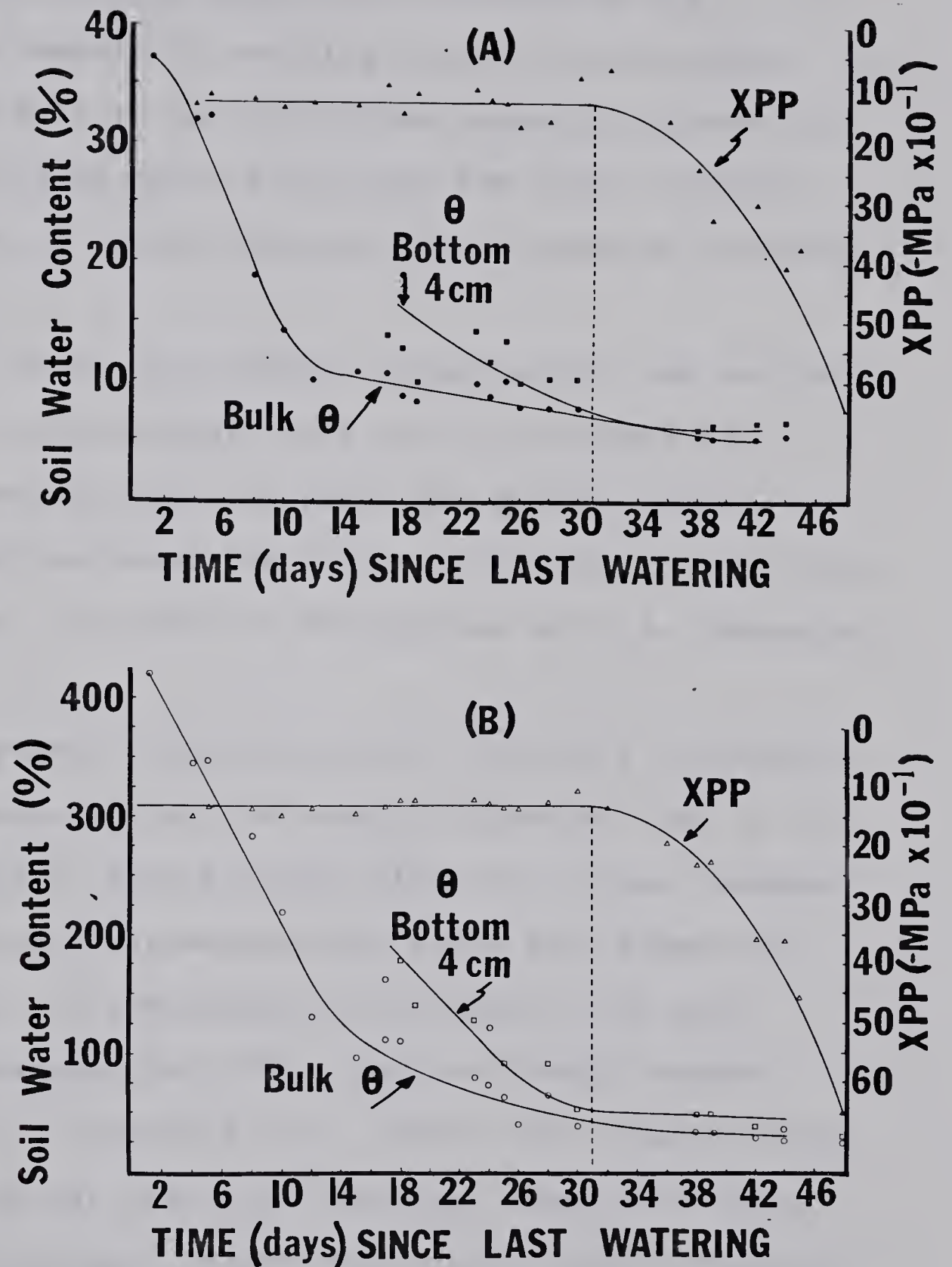


Figure 19. Relationships between time since last watering and xylem pressure potential (xpp) of three-month-old white spruce seedlings and between time since last watering and soil water content(θ) of a "greenhouse mix" (A) and a peatmoss (B).

decline in XPP judging by this study.

It therefore appears that one-month-old seedlings are more sensitive to drying soils than three-month-old seedlings. One -month-old seedlings, grown on an organic substrate were able to maintain xylem potentials above the conventional wilting point (-1.5 MPa) for longer periods after the onset of drought than seedlings grown on a mineral soil.

A direct correlation between xylem tension and survival was not found in this study. This is only possible when parts may be excised from the plant for xylem tension measurement and the remainder of the intact plant used for a test of survival. An indirect correlation is to be presented later.

Although peatmoss was originally selected to represent "duff" it is obvious from the results presented that it is not representative. Duff includes plant and animal residues at various stages of decomposition, cells and tissues of soil organisms, and substances synthesized by the soil population (Hausenbuiller 1973). Duff seriously impedes seedling survival (Crossley 1952, Endean 1972, Quaite 1956) because it dries out easily and rapidly, especially under open canopy situations. Decayed wood under shaded conditions (Hellum 1972, Lees 1964) and mineral soil in open areas (Sutton 1969, Wagg 1964) are considered the best seedbeds because they are especially moister than duff conditions allow.

(2) Survival

Seedling survival, given a certain moisture condition, is dependent on factors such as stress preconditioning (Day 1963), period of development prior to drought (Jarvis et al. 1966) and seedbed type (Place 1955). As previously stated, one-month-old white spruce seedlings were very sensitive to changes in soil moisture. This was more pronounced on mineral soil than on peatmoss.

Time since last watering was found to have a significant effect ($P \leq .05$) on seedling survival (Table 10). There were also significant differences ($P \leq .05$) in survival between types of soils used.

Table 10: Analysis of covariance for the effect of drying soils on mortality of one-month-old white spruce grown on 2 soils.

Source of Variation	Sum of Sq.	DF	Mean Square	F	P
Days	228.714	1	228.714	177.150	$\leq .05$
Soil	57.250	1	57.250	44.343	$\leq .05$
Explained	231.046	2	115.523	89.478	$\leq .05$
Residual	189.789	147	1.291		
Total	420.835	149	2.824		

Germination of white spruce under boreal field conditions began in late June and early July in one study (Rowe 1955). Recently germinated seedlings must grow their roots into mineral soil quickly in order to reach more

stable moisture conditions than duff affords. The rapidity with which soil surfaces dry is highly dependent on the surface material, peatmoss enabling seedlings to withstand longer periods of drought (13 days) than did mineral soil (3 days) before survival was affected (Figure 20). Peatmoss is better than mineral soil, judging by this study.

It appears that xylem pressure potentials can be used more effectively than bulk soil water content in predicting survival of young seedlings. According to Black (1977) a small change in the water content of black spruce [Picea mariana (Mill.) B.S.P.] seedlings resulted in lethal drops in turgor and osmotic plus matric potential. Also, a drop in bulk soil water content does not imply an immediate drop in the water content in the rhizosphere. A direct correlation can easily be determined for two- or three-year-old seedlings, while an indirect correlation must be determined for younger seedlings (Figure 20). It is important to note that the relationship between XPP and survival will vary with each soil type due to inherent differences in hygroscopic properties.

Seedling survival is more adversely affected by a drop in XPP to mineral soil than on peatmoss (Figure 20). Young jack pine seedlings, in the field, may experience XPP lower than -2.0 MPA.² This is because younger seedlings are less effective than older seedlings in closing their stomata during higher periods of high vapor pressure deficit (VPD).

²Mayo, J.M. 1979. Personal communication, Department of Botany, University of Alberta, Edmonton, Alberta.

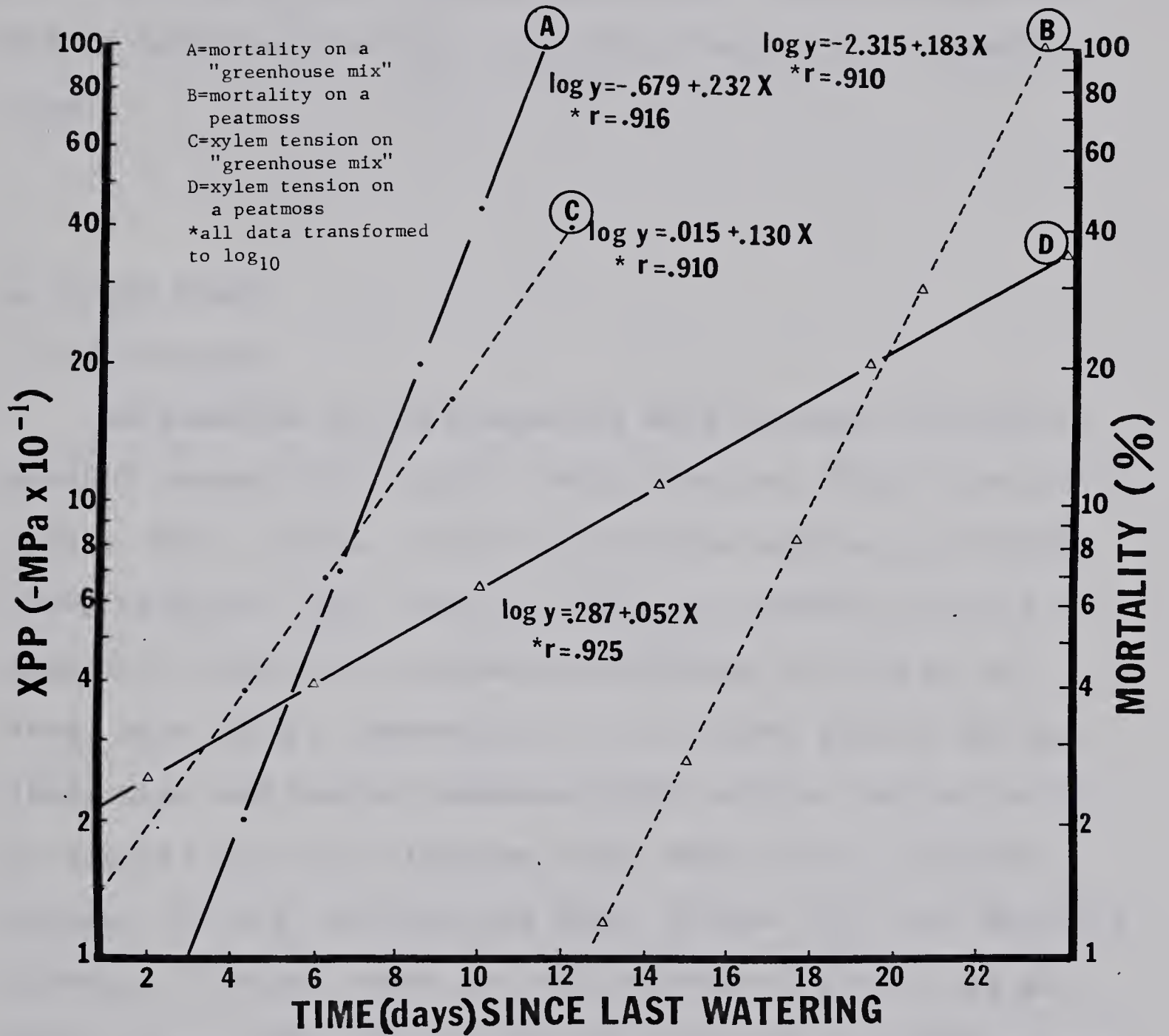


Figure 20. Relationships between time since last watering and xylem pressure potential (XPP) and mortality of one-month-old white spruce seedlings.

At -2.0 MPa xylem tensions in the field, mortality of white spruce is nearly twice as high on mineral soil as on peatmoss. The results indicate that white spruce seedlings are very sensitive to drying soils and that the effect of drying soils on seedling survival is dependent on seedbed type.

B. Field Study

1. Germination

Germination is influenced by many factors including: seedbed receptivity (Bedell 1948, Crossley 1952, Place 1955, Sutton 1969, Waldron 1966) and invading vegetation (Blyth 1955, Crossley 1955, Waldron 1966). Detrimental effects of competing vegetation include overshadowing (Jarvis et al. 1966, Rowe 1955), competition for moisture (Jarvis et al. 1966, Sims and Mueller-Dombois 1968) and the smothering of germanants by litter (Hellum 1972, Rowe 1955). Periodic drought can kill germinating seeds (Place 1955) and maintain dormancy to those seeds not yet germinated (Jarvis et al. 1966, Place 1955). Some shade often provides conditions more suitable for germination of white spruce because shade decreases rates of moisture loss (Day 1964, Place 1955). Birds and rodents can reduce the number of germinating seeds significantly (Blyth 1955, Crossley 1955, Rowe 1955, Waldron 1966). Insects and disease may also influence germination success (Sutton 1969).

Germination rates vary significantly ($P \leq .05$) with (1) site, (2) seedbed, (3) time of year, and (4) site X time interaction (Table 11).

Table 11: Analysis of variance for germination success of white spruce on three seedbed types in each of an uncut and clearcut area.

Source of Variance	DF	Mean Square	F	P
Site	1	1.467	16.20	$\leq .05$
Seedbed	2	0.886	9.78	$\leq .05$
Site X Seedbed	2	0.666	7.36	$\leq .05$
Nested (Site X Seedbed)	144	0.090	-	
Time of year	2	0.243	42.91	$\leq .05$
Time X Site	2	0.020	3.58	$\leq .05$
Time X Seedbed	4	0.002	<1	
Time X Site X Seedbed	4	0.0076	1.34	
Error	288	0.0057		
Total	449			

The differences in germination rates between the uncut area and the clearcut area were obvious (Figure 21). The mean germination rate was 8.3 percent for the uncut area and 2.0 percent for the clearcut area (significant at $P \leq .05$).

Disturbed plots, that is, those where mineral soil was exposed or competition removed, yielded more germinants than control plots (Figures 22A and 22B). The difference was much clearer for the plots in the reserve stand.

In Alberta, germination appears to commence in late June or early July (Crossley 1949, Rowe 1955) and peaking in

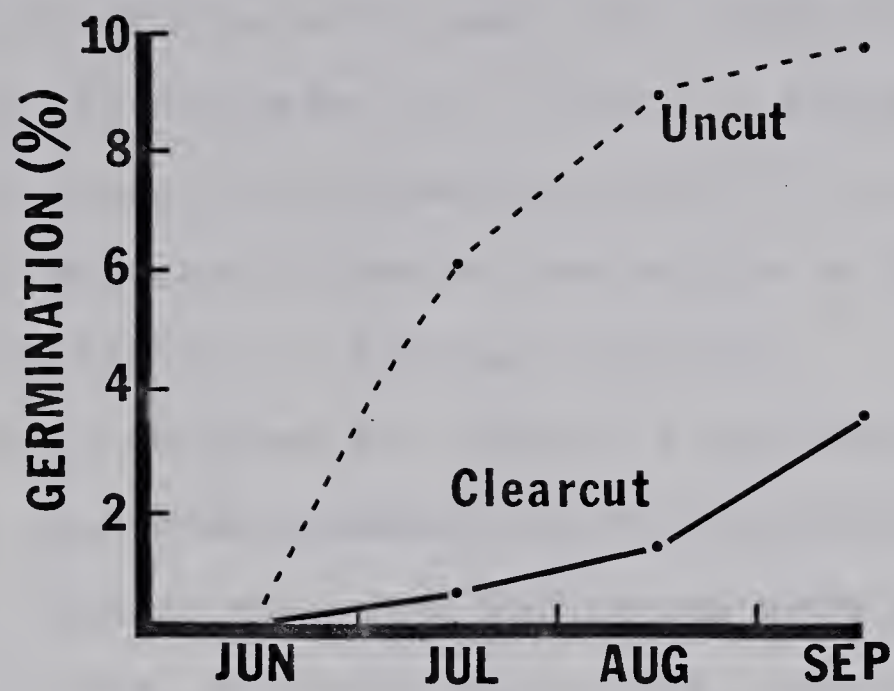


Figure 21. Cumulative germination rates for white spruce on 2 sites.

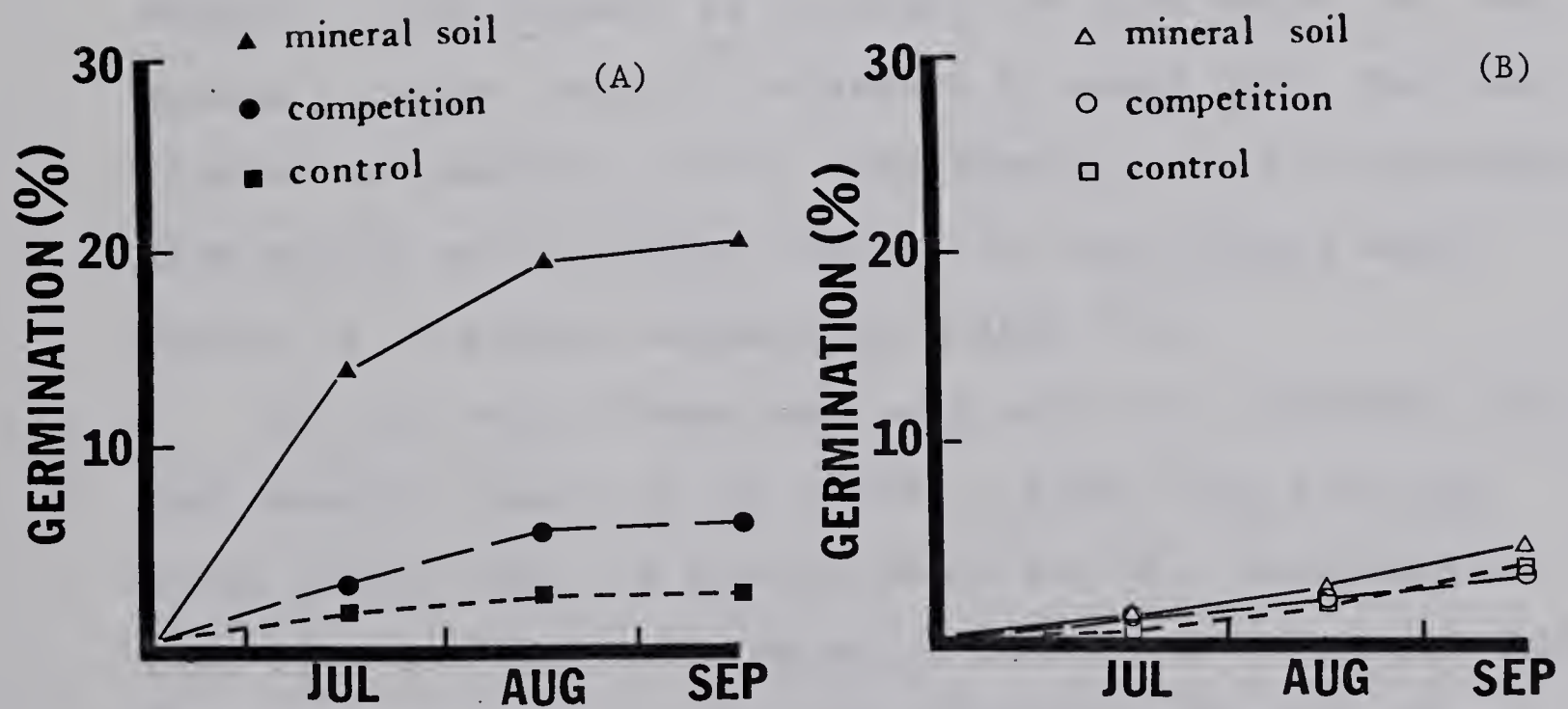


Figure 22. Cumulative germination rates in an uncut area(A) and a clearcut (B) for 3 seedbeds.

July (Jarvis et al. 1955) when prevailing weather permits. The results of this study show that germination began in late June and continued into August or early September. There was enough precipitation in 1977 to allow for continued germination during the months of July and August when precipitation is normally limiting.

Shading improves the chance of germination because it protects seed from excessive heating and rapid drying. However, seedbed type also influences germination (Ackerman 1957, Day 1963, Eis 1965, Place 1955, Quaite 1956, Rowe 1955). Thick duff layers seriously impede the establishment of spruce regeneration and competition for light, water, and nutrients contribute to failures in establishment (Blyth 1955, Rowe 1955).

In general, germination can take place and lead to seedling establishment if seedbeds are kept moist for long enough to allow roots to establish in moist soil. The more friable the seedbed and the more likely it is to experience fluctuating soil moisture content the less likely white spruce is to become established (Table 12).

In this study there were many potential problems. With only monthly visits to the field, a great deal may have taken place, that was missed. Seeds may have germinated, then died and were never counted. Therefore, I assumed that the number of newly germinated seedlings missed, for any reason, remained constant for both sites over time. I also assumed that ingress from surrounding areas was minimal.

Table 12: Number of plots which produced no germinants

Seedbed Type*	Site	
	Reserve	Logged
MC	8	12
CO	12	14
C	16	15

* MC = mineral soil exposed
CO = competing vegetation removed
C = control

According to Quaite (1956) and Rowe (1955) from 100m to 120m is the maximum distance from the seed source for adequate spruce seed dispersal. The plots in the clearcut were 200m from the nearest seed source. It is possible that some regeneration in the uncut area was attributable to the natural seed source. However, it is doubtful that this would have resulted in the four fold difference in percent germination between the clearcut area and uncut area (Figure 21).

2. Survival

Time of year and site (clearcut versus uncut stand) were found to have a significant ($P \leq .05$) effect on the survival of first- and second-year seedlings in the field (Table 13).

It was not clear from the data presented if rates of survival had stabilized after two years (Figure 23). The

Table 13: Analysis of variance for field survival of first and second-year white spruce seedlings on 3 seedbed types in each of an uncut and clearcut area.

Source of Variance	DF	Mean Square	F	P
Site	1	14638.996	12.726	≤.05
Seedbed	2	1152.238	1.002	>.05
Age	1	25675.242	22.320	≤.05
Site X Seedbed	2	1605.810	1.396	>.05
Site X Age	1	2683.819	2.333	>.05
Seedbed X Age	2	1464.753	1.273	>.05
Site X Seedbed X Age	2	279.538	0.243	>.05
Explained	11	4456.289	3.874	≤.05
Residual	122	1150.311		
Total	133	1423.738		

decline in survival rate was reduced during the second year, indicating that second-year seedlings had increased in hardiness. The survival rates over winter and throughout the second year appeared to be similar for both sites (Figure 23). Improved survival on the clearcut during the first year was not surprising. The debris associated with clearcutting provided adequate shading for seedling establishment yet allowed sufficient light penetration for growth.

Most of the estimated mortality, on both sites occurred as a result of drought. Survival during the first year was highest on the control plots and lowest on mineral soil

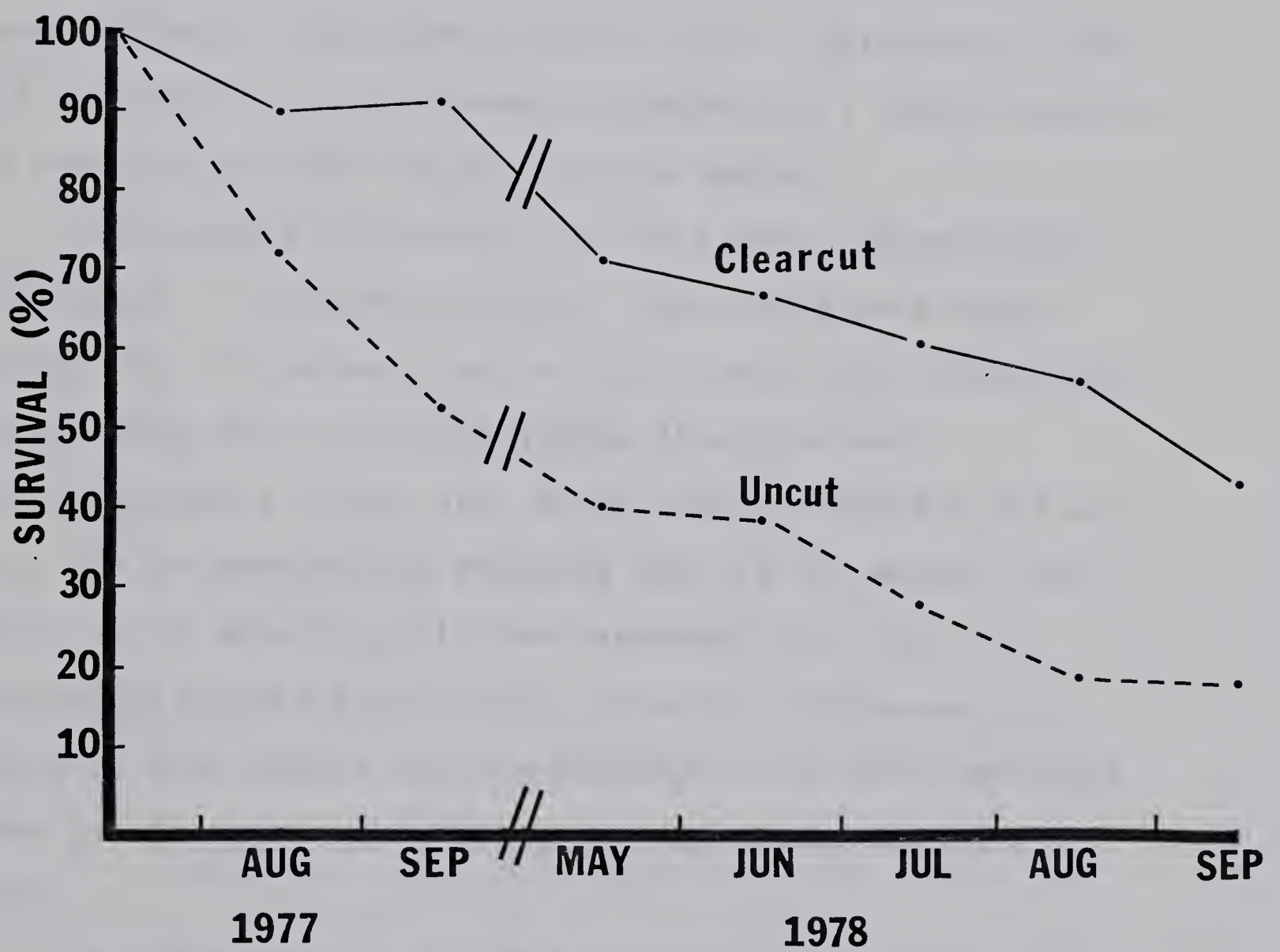


Figure 23. Survival of first- and second-year white spruce seedlings on an uncut and a clearcut area.

plots and plots with competing vegetation removed (Figures 24 and 25). By the end of the second year survival on the control plots was poorest. During the first year when precipitation was abundant, therefore, the competing vegetation on the control plots competed mostly for available light. Some shade has been shown to increase early rates of survival explaining better rates of survival on control plots during the first year. In the second year a combination of poor growth due to lack of sufficient light and low precipitation probably resulted in a severe decline in seedling survival on the control plots.

The results indicated that there was no significant difference in survival of first- and second-year white spruce due to seedbed type but that there were differences in stocking due to seedbed (Table 14). Sims and Mueller-Dombois (1968) also found that germination did not vary due to seedbed but stocking did. By the second year, stocking on mineral soil plots exceeded both that on competition plots and control plots. The difference in stocking may reflect the disadvantage to seedling survival that is imposed by the duff layer especially during a dry year.

Of those factors believed to influence survival of spruce seedlings it is my belief that good plant-soil water relations are the key to successful regeneration. Good water relations are manifested under shaded conditions or seedbeds of decayed wood or mineral soil or both.

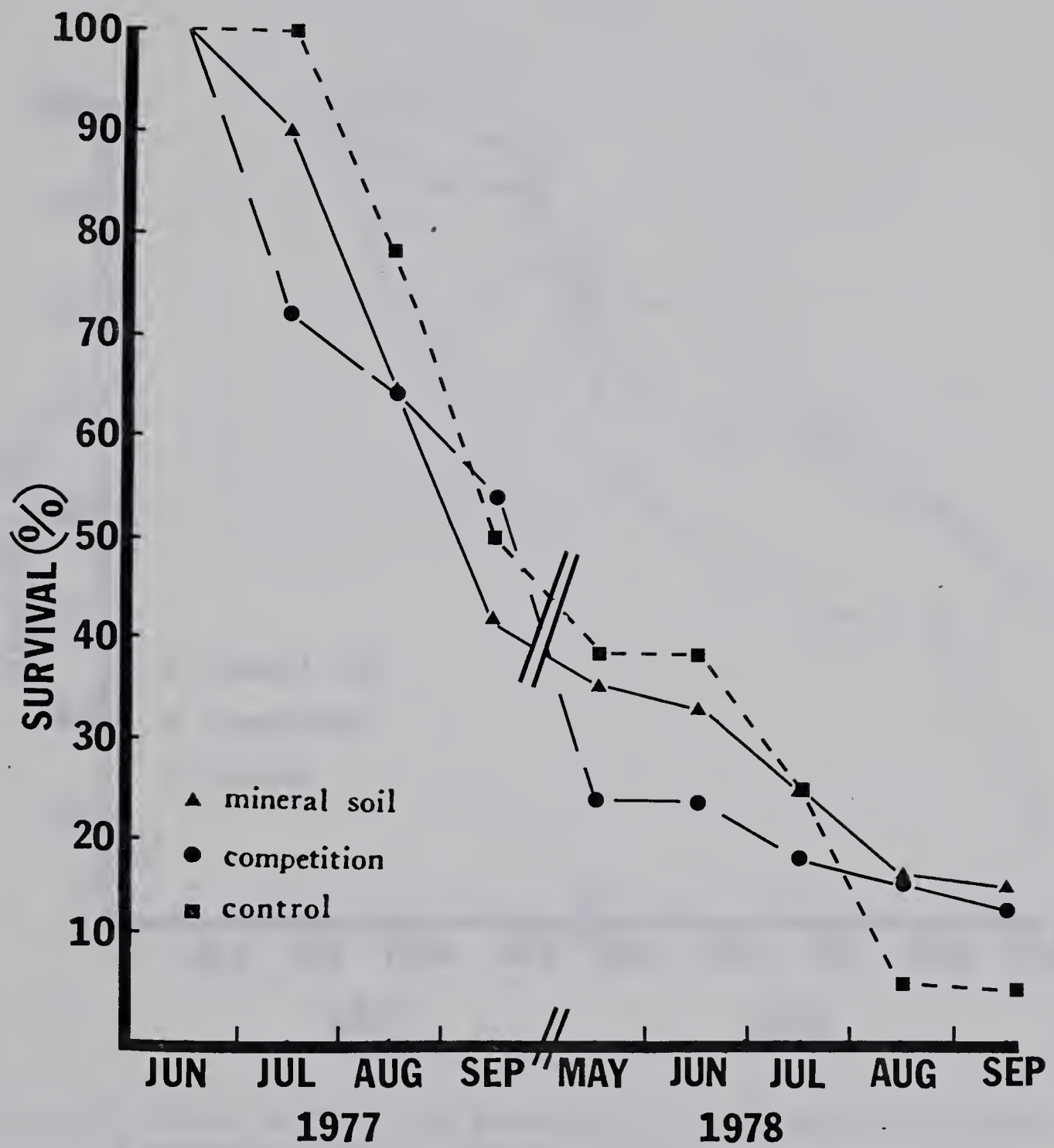


Figure 24. Survival of first- and second-year white spruce seedlings for 3 seedbed types in an uncut area.

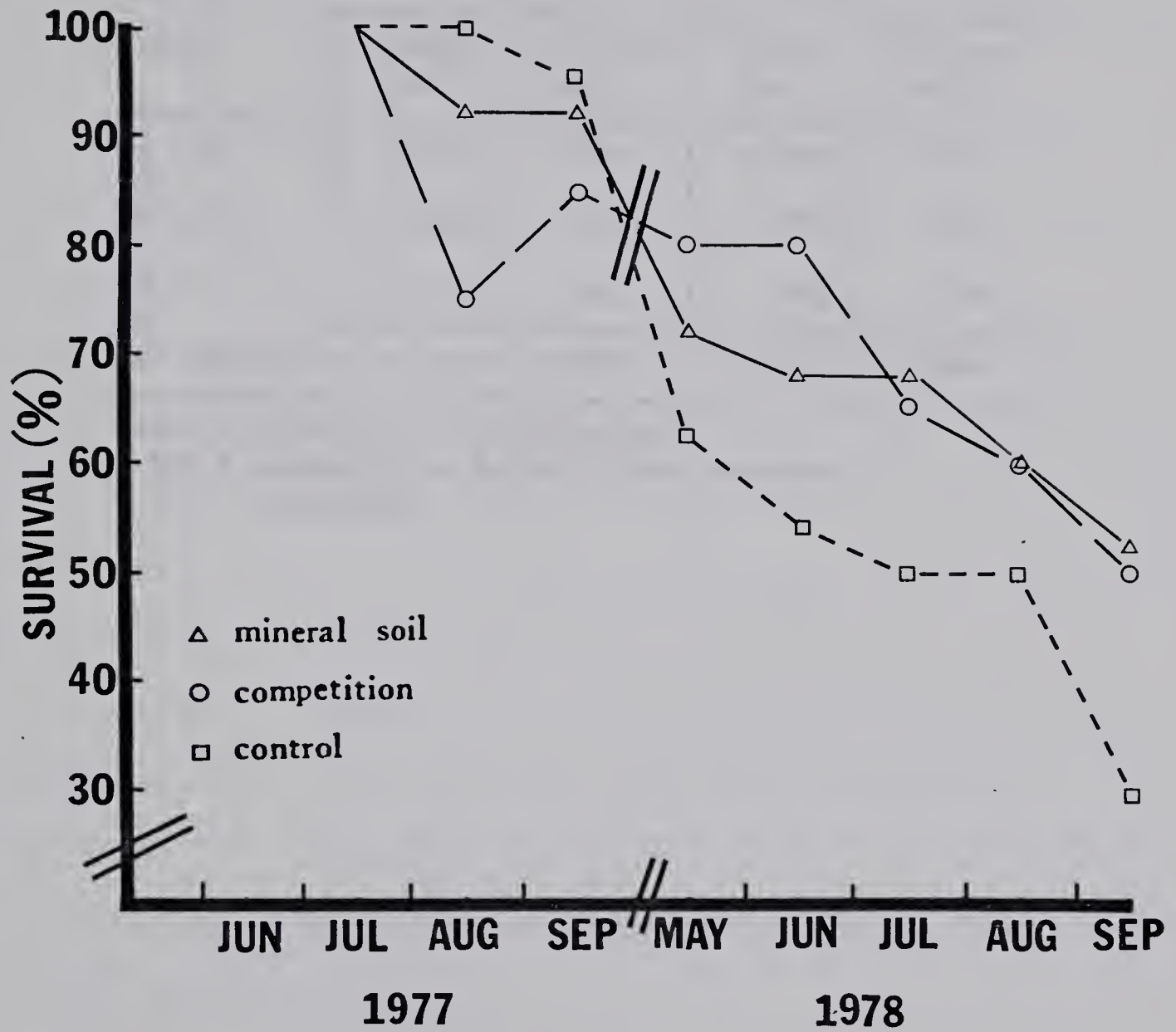


Figure 25. Survival of first- and second-year white spruce seedlings for 3 seedbed types in a clearcut area.

Table 14: Stocking of first- and second-year white spruce, in terms of number of seedlings per unit area, on 3 seedbed types* in an uncut and a clearcut area.

YEAR		SITE			
		LOGGED		RESERVE	
		FIRST ha ⁻¹	SECOND ha ⁻¹	FIRST ha ⁻¹	SECOND ha ⁻¹
S	MC	2272	1284	6126	2371
E					
E	CO	1680	988	1976	494
D					
B	C	2272	692	790	99
E					
D	TOTAL	6224	2964	8892	2964

*MC = mineral soil exposed

CO = competing vegetation removed

C = control

IV. SUMMARY

The main objective of this study was to compare success of one-and two-year-old white spruce seedlings in cutover and uncut areas and describe some ecophysiological characteristics which influence success or failure (Figure 26).

Retention of carbon-14 in first-and second-year seedlings followed distinct seasonal patterns, with peak retentions in August. Together, light and watering significantly ($P \leq .05$) altered these patterns. The individual effects of light and watering on retention were more evident on first-year seedlings than on second-year seedlings. Rates of retention were lowest when plants were stressed or grown under full-light conditions.

Generally, second-year seedlings translocated a higher percentage of ^{14}C to the roots than did first-year seedlings. The individual effects of light and watering on translocation were not clear but interacted to alter the patterns significantly.

Between June and September much of the recently photoassimilated carbon-14 was channelled into storage rather than into structural components in first-year seedlings. Second-year seedlings deviated from this pattern. In July, an increase in the insoluble fraction corresponded with a period of rapid growth. Although one might expect both light and watering to alter these patterns, the results

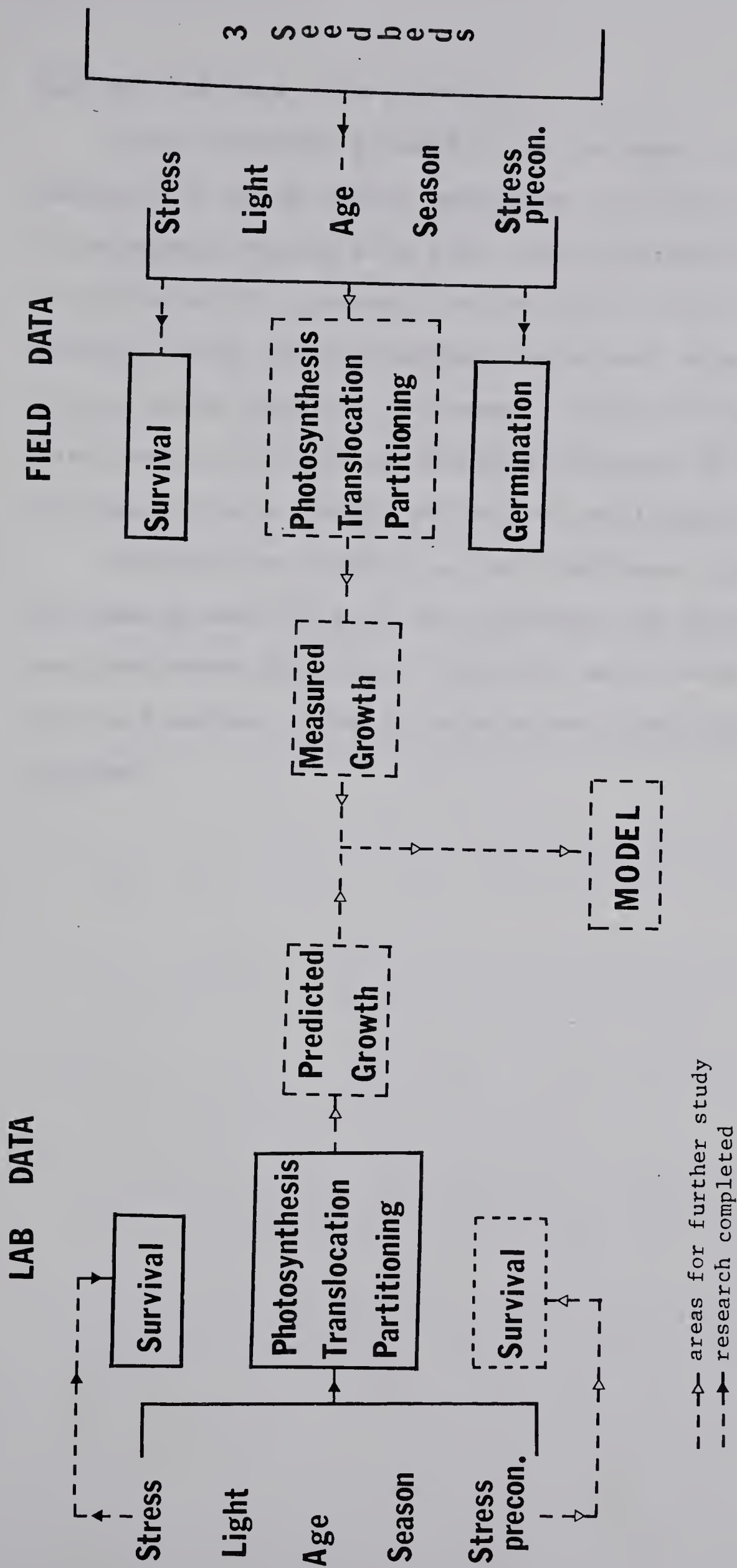


Figure 26. An overview of the research carried out and further research needs on white spruce regeneration.

did not indicate this clearly.

Xylem pressure potential can be used to estimate survival of white spruce seedlings on drying soils. The relationship varied with soil type, probably due to differences in hygroscopic properties of the soils. One-month-old spruce seedlings were much more sensitive to drying soils than were three-month-old seedlings. This may have been due to the increased efficiency of older seedlings to close stomata during periods of prolonged water stress.

Germination success in the field was highly dependent on shading and survival was dependent on adequate light and soil moisture. Favorable light and water were best provided in the clearcut on shaded microsites with the mineral soil exposed.

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